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A Central Australian Ochre Mine

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ABSTRACT. An ochre mine still used by Warlpiri men in central Australia is described, and its relationship to trading networks, mythology and control over access is discussed. The paper also examines the methods of mining and processing the ochre, and describes some task-specific stone tools used in mining. Many similarities are apparent between this mine and two famous large ochre deposits, Parachilna and Wilga mia, neither of which is currently in use.

It is of particular interest for three reasons: there are stone tools used specifically for quarrying the deposits; the entire mine is an underground chamber; and it provides ethnographic evidence on the complexities of the control of such valued resources.

PETERSON, NICOLAS & RONALD LAMPERT, 1985. A central Australian ochre mine. Records of the Australian Museum 37(1):1–9.

KEYWORDS: Aborigines, anthropology, prehistory, ochre, mining.

Red ochre is one of the most important minerals mined by Aboriginal people. It is used as a pigment for a variety of artistic and decorative purposes: it adorns the human body during ceremonies; it is one of the main pigments used in rock art; and many items of wood and stone, including some shields, boomerangs and clubs, are liberally coated with it. The antiquity of its use throughout Australia is demonstrated at a number of archaeological sites. At Kenniff Cave in Queensland, red ochre was found in all levels dating back to the earliest occupation some 19,000 years ago. It was also found in basal levels of similar age at other sites including Miriwun in the Kimberley district of Western Australia, sites in Arnhem Land, and Cloggs Cave in Victoria (Mulvaney, 1975: 155). But the earliest, and most spectacular, evidence for its use comes from the Lake Mungo site in western New South Wales where the body of a man who died some 30,000 years ago had been coated with red ochre at the time of burial (Bowler & Thorne, 1976: 129).

Usually, red ochre is dug out of the ground from small pits, in nodule form. Although ochre deposits are common throughout the continent, certain kinds of red ochre are more highly valued than others and are important in Aboriginal mythology. In the case of the Parachilna mine in the northern Flinders Range, red ochre, said to be the blood of a sacred emu, was famous over a wide region of central Australia. It was so eagerly sought that Dieri speakers living 500 kilometres to the north sent armed parties of 70–80 men through hostile territories in order to barter for ochre from the mine's owners (Howitt, 1904: 711). To such people, Parachilna ochre was "considered the 'proper' ochre and is that which is always used, although plenty, hundreds of miles nearer, could easily be obtained" (Horne & Aiston, 1924: 34). It is possible that the Dieri needed the ochre, not only for their own ritual purposes, but also to use in trade with people to the north from whom they obtained pituri (see Watson, 1983: 31–32).

Usually, these highly valued ochres have a silvery sheen caused by an admixture of some other element such as free mercury (cinnabar) in the case of the Parachilna (Bookatoo)[1] ochre deposits, or tiny fragments of mica in the case of the deposits described here. These more valued deposits, the two best known of which are Wilga mia in Western Australia and Parachilna, have been quarried on a grand scale.

The scale of excavations, quite apart from the ethnographic evidence, suggests that the material must have been widely traded, reflecting the significance of red ochre throughout the continent, including Tasmania (Robson & Plomley, 1982). The Wilga mia open cut excavations, for instance, are between 15 and 30 metres in width and up to 20 metres deep, with chambers around the bottom (Davidson, 1952: 82–83), in an area with an estimated population density of only one person per 52 square kilometres. Similarly, the Parachilna mine is an open cut type measuring some 12 metres by 23 metres with six tunnels into the hillside, all but one of which has caved in (Broughton n.d.). While in both these cases regular exploitation of the deposits appears to have ceased by early this century, the mine to be

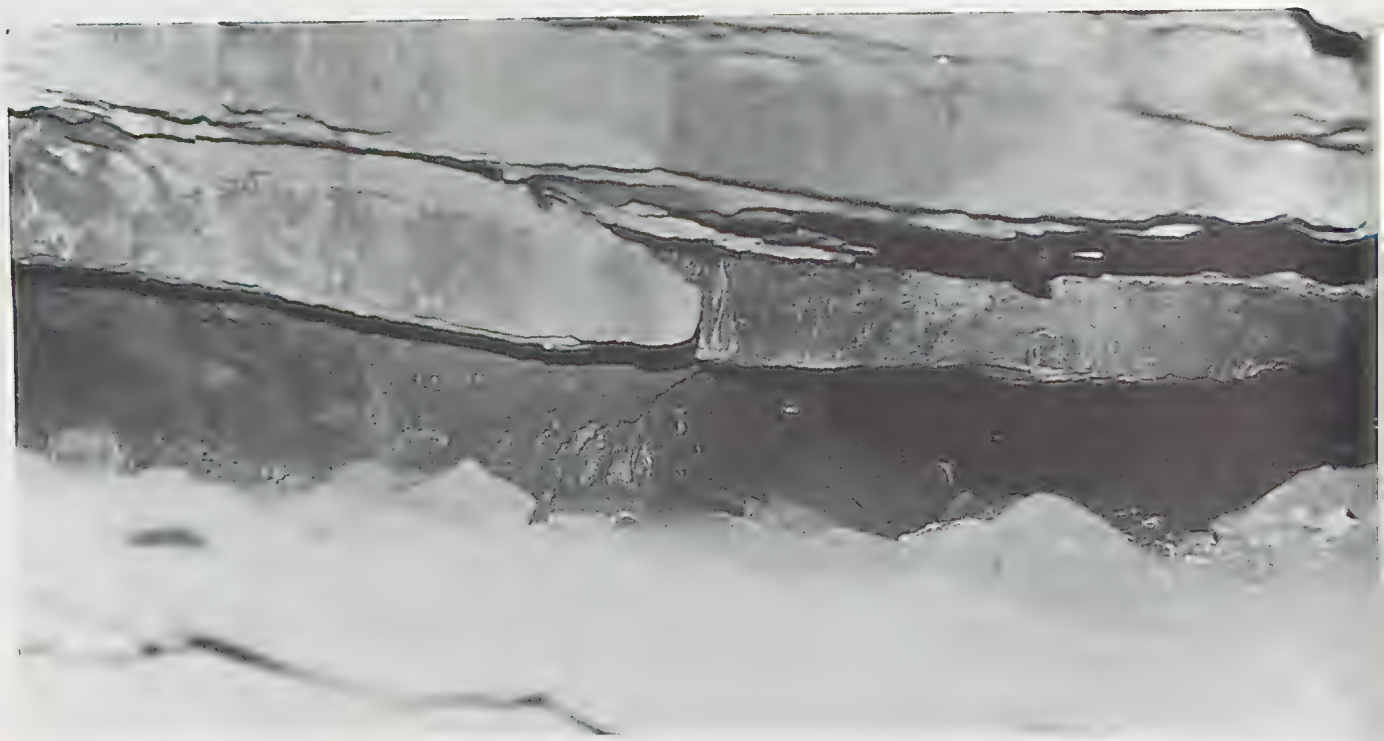


Plate 1. The beginning of the northern shaft from the middle of the central chamber.

described here is still in use. It is of particular interest because there are stone tools used specifically for quarrying the deposits, and the entire mine is an underground chamber.

The Central Australian Mine

The mine is located in the Campbell Ranges in the southern portion of Warlpiri country. As elsewhere in the region, the ranges are a white and pink quartzite which is tough, thickly bedded with basal coarse, pebbly, hematitic sandstone and pebble conglomerate (Wells, 1972: 6), originally deposited in a shallow marine environment. There is a small fault in the region of the mine and, although the geological map shows horizontal bedding, the mine entrance slopes down at approximately 25° in apparent conformity with the bedding of some of the surrounding hills. The deposit itself is a soft specular hematite bedded in conformity with the bedrock in a seam about a metre thick.

Located near the top of a low hill, the entrance to the mine is a small hole, 1.0 x 0.6 m, that leads directly into the central chamber. Figure 6 provides a sketch plan of the mine. The central chamber is approximately 9 x 12 x 1 m and off this, running almost due north, is a horizontal shaft 20 x 5 x 1 m (see Plate 1). To the south of the central chamber is a second, smaller chamber approximately 6 x 6 x 1 m. The empty space measures approximately 240 cubic metres and appears to have all been originally occupied by the ochre ore so that approximately 300 tonnes have been removed. Nowhere are there any roof supports, nor do there ever appear to have been any. The only sign of a roof fall is a large slab, directly inside the entrance, over which one crawls when entering the central chamber (see Plate 2).

The ochre deposit extends from floor to ceiling. Today it is worked with the aid of electric torches and small metal axes, hammers or metal digging sticks. The miners kneel on their heels or sit cross-legged in front of the face and hack at it with the axe, hammer or stick to create a pile of lumpy powdered ore in front of them (see Plate 3). Sometimes it comes away in quite large consolidated blocks. In the past, people lit fires inside the mine, and charcoal and pieces of wood can be seen on the floor in Plate 4. It would be possible to work the central and even southern chambers without artificial light at a pinch, but not the long northern shaft. In the past, stone choppers were used to hack at the ore, and these now litter the floor.

Five of the tools were taken for closer examination (Figs 1–5). The lack of either formal shape or edge preparation shows that they are simply naturally fractured blocks of quartzite, probably from the scree slope just outside the mine's entrance, chosen because they have reasonably sharp edges and are of adequate weight. The entire surface of each tool is coated with red ochre and the edges are heavily damaged through use. Typically, this use damage takes the form of haphazard, bifacial flake scars along the working edge, accompanied by a dull polish at the very apex of the edge (Plate 5). Under magnification, this gloss is seen to be made up of the polished surfaces of thousands of individual quartz grains; no striations are visible. Resulting from use damage, the flake scars are highly varied in size, shape and spacing. This is quite unlike the even pattern of flake removal from deliberately

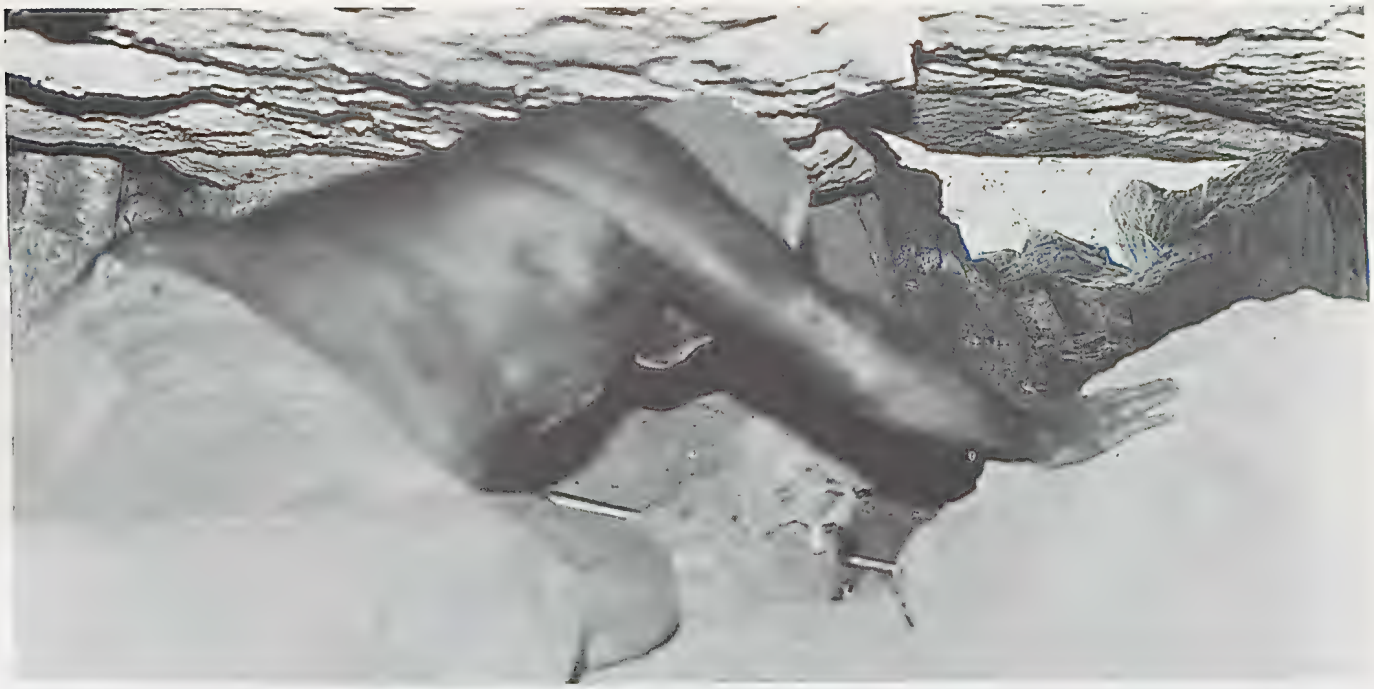


Plate 2. Crawling towards the entrance over the roof fall.

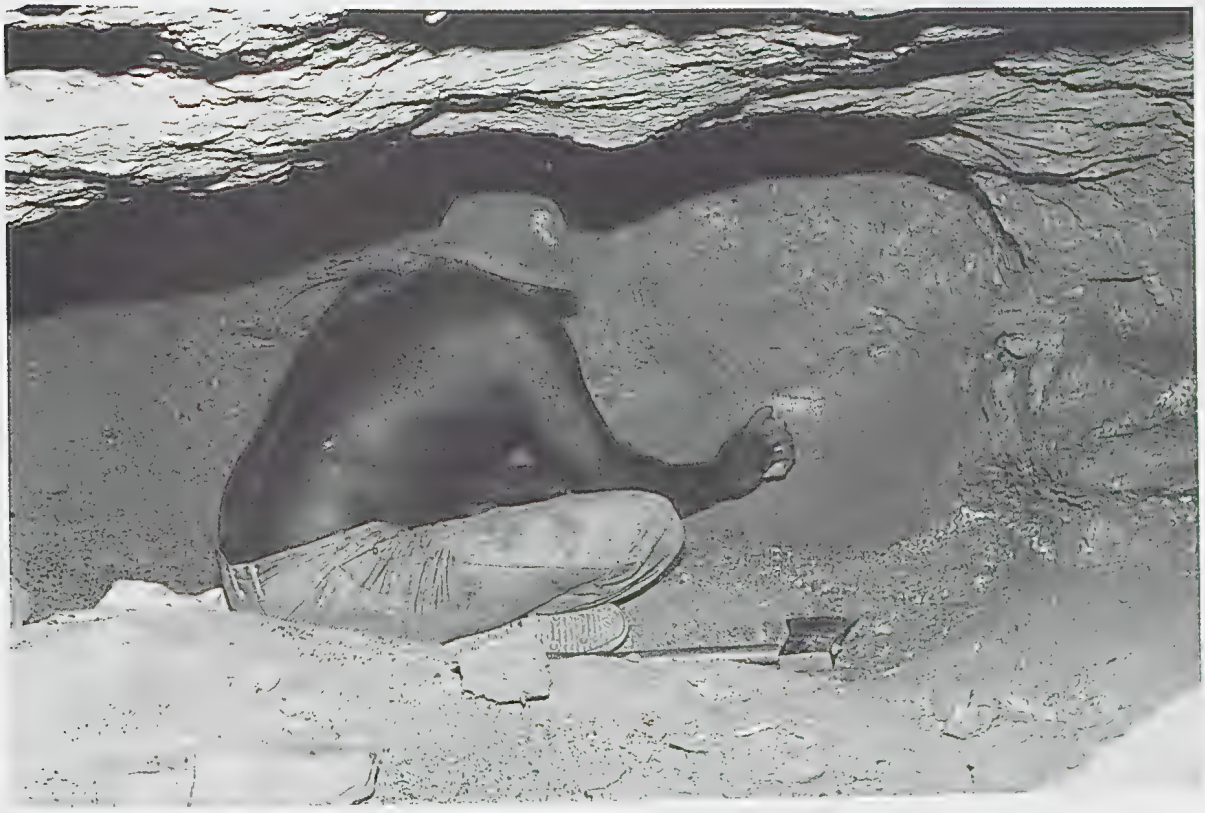
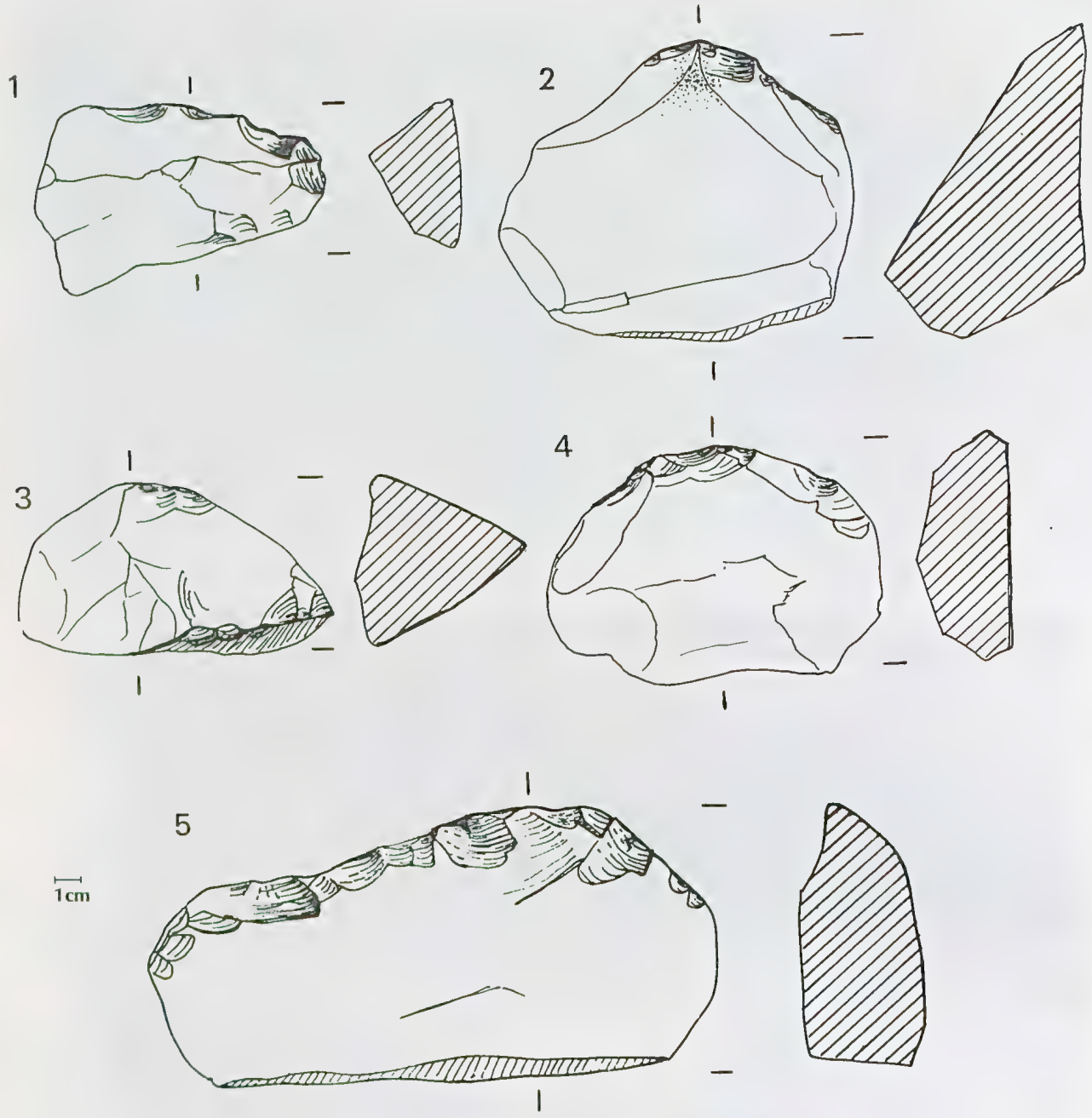


Plate 3. Jampijinpa has put down his metal axe and taken up a quartzite block from the floor to pulverise the ochre so that he can ascertain the quality of the ore at this spot.



Figs 1–5. Five stone choppers used for quarrying the ochre.

prepared edges. The basic measurements of the five stone tools are set out in Table 1:

	Length (mm)	Breadth (mm)	Height (mm)	Weight (gm)	Edge Angle
1	144	103	43	800	81
2	130	86	67	600	75
3	158	126	80	1740	77
4	233	114	62	1830	86
5	149	104	76	1100	88

The general characteristics of the tools and their location on the floor of the mine are reminiscent of Wilga mia:

"In the tunnels and strewn upon the bottom of the open cut are hundreds of crude, unshaped stones, two or three times the size of the fist, which still serve as hand mauls for battering away the solid matrix in which the prized ochre is imprisoned" (Davidson, 1952: 83).

Mined ore is today placed in flour or sugar bags and plastic buckets. In the past it was carried in deep wooden dishes, *ngami*, used for transporting water, or temporary bark dishes created from the bulbous growths

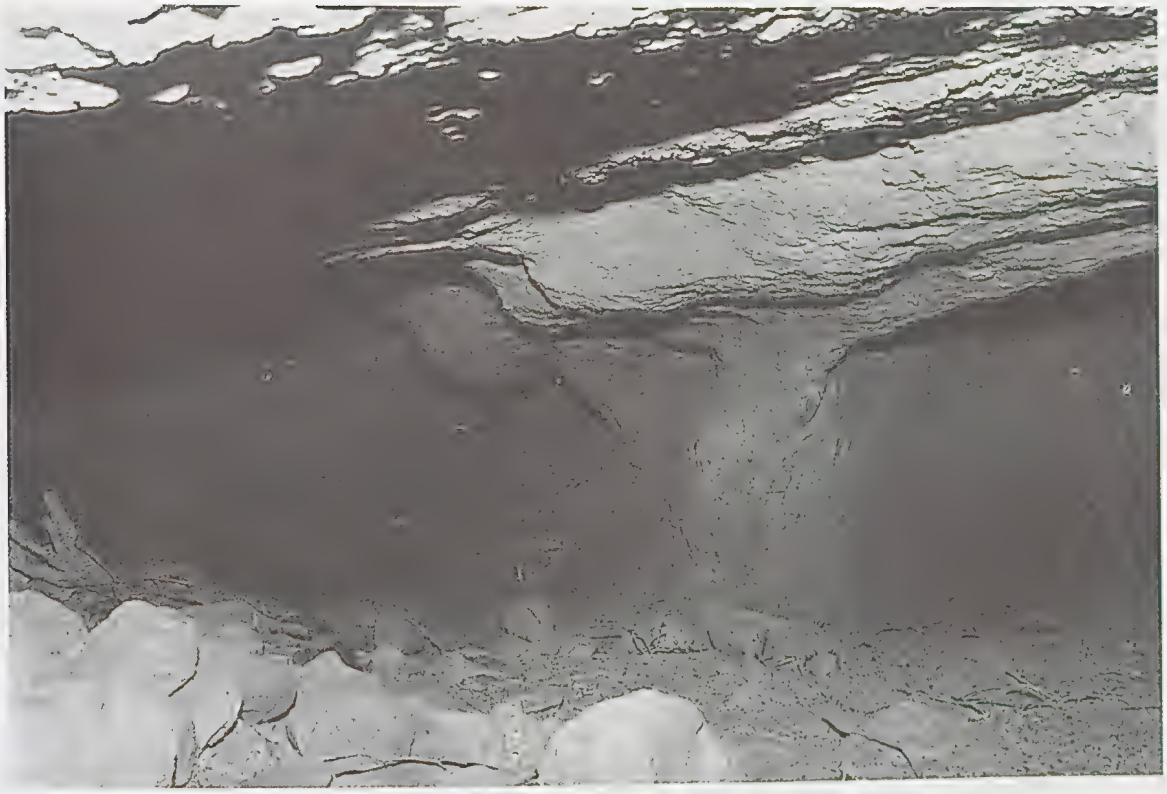


Plate 4. The seam of ochre can be clearly seen running from floor to ceiling. Unburnt sticks and chunks of quartzite cover the floor. This is the southern chamber.

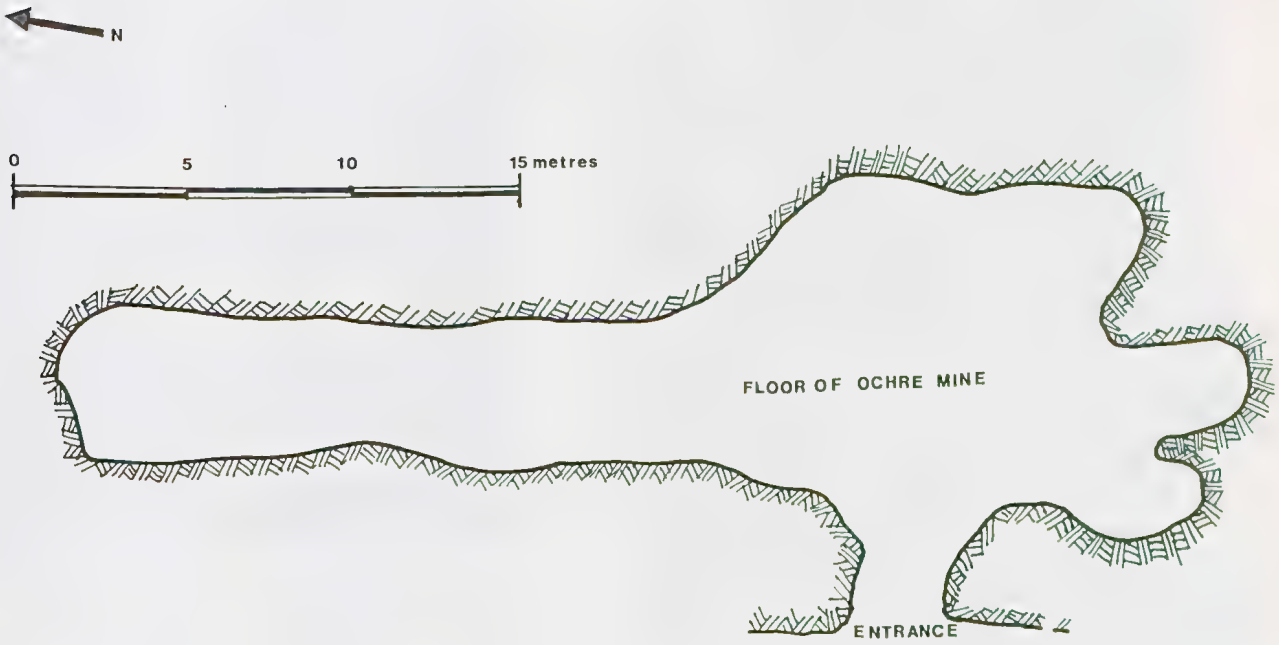


Fig. 6. Sketch plan of mine.

on the side of large eucalypt trees. It is clear from the three grinding grooves immediately outside the mine entrance that it was not unusual for initial treatment of the ore to take place on the spot. This involved simply grinding the ochre into a fine powder by hammering and rubbing. Because any minor impurities or slightly inferior ochre would be left behind, such a practice would mean that more ore could be carried away. Back in camp the ochre is further treated by mixing with a little water and made into balls or cakes called *kapardu*. Kimber reported that in 1932, or thereabouts, the balls were wrapped in ti-tree bark forming bundles slightly smaller than a basket ball (Kimber, letter 18 March, 1980).

This process is similar to that used by the Dieri when preparing Parachilna ochre for transportation. After excavation the ochre was mixed with water, shaped into 'loaves' about 8 kg in weight, and dried (Curr, 1886: 70).

The amounts collected by individuals, on the occasions when one of the authors has been present at the mine, ranged from 2 to 22 kg, averaging some 7.7 kg. An average size *ngami* dish measuring 50 x 18 x 13 cm (approx.) holds about 7 kg of powdered ochre and is a difficult load to carry down the hillside from the mine. Although it is not possible to obtain any accurate idea of the frequency of visits to the mine, on the basis that four people visited it twice a year and each obtained 7 kg the mine would have been in use for around 5,600 years.

Usually, it is men that quarry the ochre, and although no women are known to have been in the mine for the previous twenty years, a Nampijinpa woman of high ritual status entered the mine to collect ochre in 1983 in company with some Aboriginal and Europen men and a female anthropologist. Older men recalled that some of their female relations had quarried ochre in the past.

Local distribution of ochre. On returning from a visit to the mine in 1972 six of the seven Aboriginal members of the party, all men, gave the ochre to a range of relatives, as set out in Table 2. In all cases these were close relatives with the emphasis on members of the wife's matriline (*jurdalja*) and the wife's father, with each man giving to approximately six other people including wives and sisters. It is not known what variation there was in amounts given.

Ochre is widely exchanged today as it was in the recent past. Prior to the second world war it was exchanged for spears from the Erhenberg Ranges to the south, coming along what Terry (1934: 506) describes as a well defined route from Salvation Rockhole 32 kms, or so, east of these ranges, to the Campbell Ranges. To the north, it was exchanged for boomerangs, shields, large mulgawood fighting spears and hair string.

Linguistic relationships. The term commonly applied by the Walpiri to ordinary red ochre is *yurlpa* but this is not the term used for the ochre from the mine. This ochre is called *Karrku* which is the term used for red ochre by the Dieri (Dijari), Guyani, Ngamani and Yarluyandi, and cognate with the Arabana and Wangururu (Wongkanguru) term according to Luise Hercus (letter 27th April, 1983). George French Angas (1847: notes to Plate XXIV) reports the same term in use on the Onkaparinga River, east of Adelaide. The distance, as the crow flies, from the Warlpiri mine to Adelaide is over 2,400 kms, and to Leigh Creek, in the heart of Guyani territory, is over 1,100 kms. The linguistic evidence suggests links between these widespread groups in the past, but whether actual trade between them was involved is unknown.

Mythology. Before entering, it is common to call out to the old heroic ancestor inside the mine 'Don't be unpleasant to us'. On one occasion a man added, 'we only want a small amount' and on another it was emphasised that they had a European with them. There are some practical dangers, as the roof fall indicates, and the presence of snakes in summer and spiders is mentioned by the people. Although Lampert crawled to the end of the northern tunnel, on a later occasion Peterson was warned from going down it as a deceased Jampijinpa's spirit was said to be there and the whole tunnel was out of bounds.

The mythology associated with the mine is complex. The deposit was created by a Warlpiri man who stole ochre from an Alyawarra deposit, east of the Stuart Highway, and brought it west. The Alyawarra deposit was the congealed blood of a slaughtered man. On his journey home, the Warlpiri man stopped first at Warrinjirrinjirri (Crown Hill on Mt Allan Station), building a hut and placing the ochre on top. He stopped again at Yariyarriri, east of Newhaven Station, building a hut there too but this time he did not place the ochre on the roof. At the site of the mine he built a hut, placed the ochre on top and then went hunting, killing an eagle (*warlawurru*) and a python (*yurnturrkunyu*) which he cooked at a windbreak nearby. Almost all recounters of this story are agreed that this man was of the

	W	WB	WMB	WFZ	WF	MBS	M	MMB	S	B	Z
1	1	1	1	1	1	1	-	-	-	-	-
2	1	-	1	2	1	-	-	-	-	-	-
3	-	-	2	-	-	-	-	-	-	1	-
4	-	-	2	-	2	-	-	-	-	-	2
5	1	1	-	-	-	-	-	-	2	1	-
6	-	1	4	-	-	1	1	1	1	-	2

Table 2. Relatives to whom six men gave ochre on return from the mine. (Each number refers to number of relatives in that class)

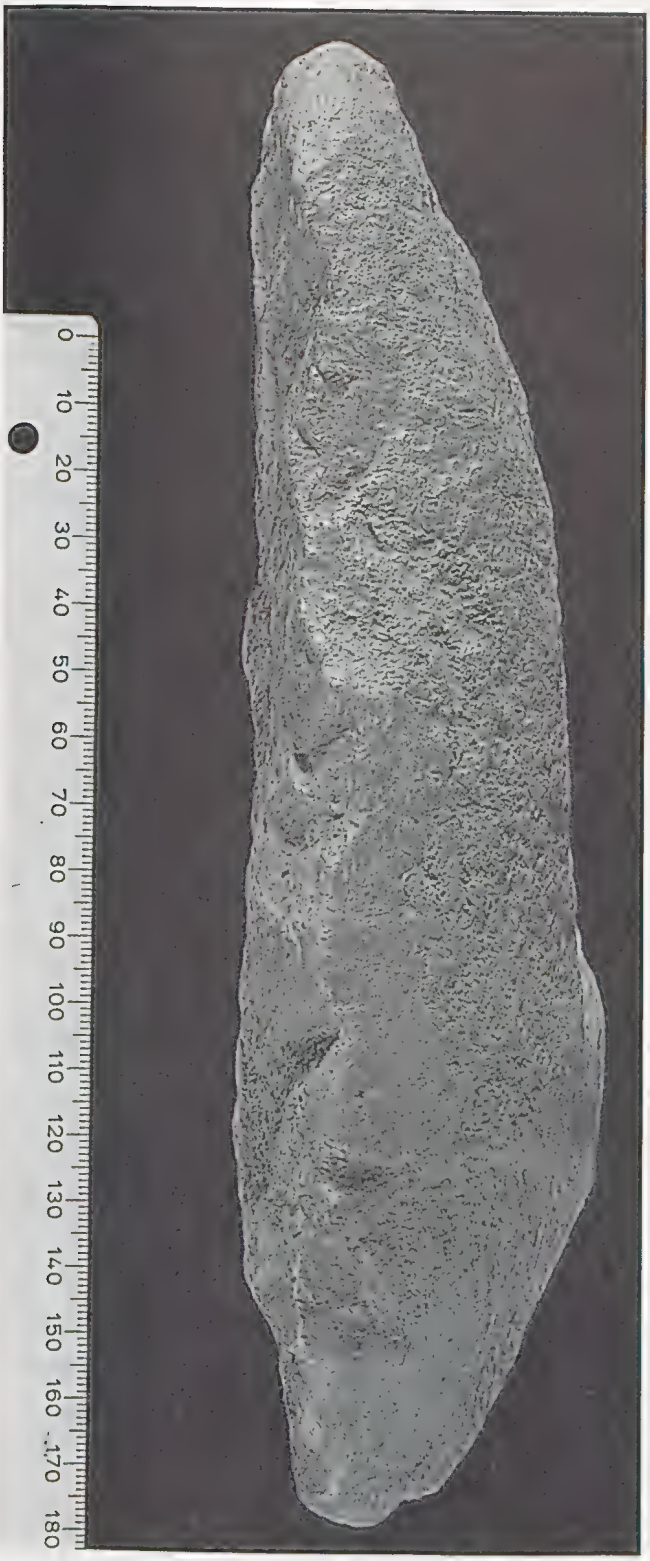


Plate 5. A detailed view of the use damaged edge of one of the choppers. The sheen on the chopper comes from the ochre.

Jupurrula subsection (except the senior man of the Jampijinpa estate in the area, who said on one occasion that the man was Jampijinpa) and had removed the ochre from his head when he saw the rain dreaming coming from the west. Jupurrula returned to the hut/mine and entered it in the evening. Two women, Napaljarri and Nungarrayi, arrived from the west. They drank water at a small rockhole on top of the hill. The hill started to grow upwards so they threw a rope around it to hold it back but the top of the rock came tumbling down. The hill grew because it smelt the sweat of the two women. A Jampijinpa-Jangala rain dreaming, all tellers agree, came from the west, passing over the mine site. One elderly Jupurrula man commented that the two dreaming women tried to feel for the sources of the water that flowed down from the two rockholes on top of the hill. The rain dreaming went east to Gurner Bore and Mt Wedge before turning north to Kulpurlurnu.

Ownership. The mine site lies on the border of a Jampijinpa-Jangala and a Jupurrula-Jakamarra estate. While it is certain that permission has to be sought for access to the mine, there is some uncertainty whether this is the exclusive prerogative of the senior males of one or other of the estates, or shared between them. The fact that the mine lies on the intersection of several dreaming tracks, and that there are two implied origins of the ochre which attribute it to different sections of the same moiety, further complicates the issue, and raises the possibility of competitive assertion of rights to control access.

Peterson has visited the mine on three occasions between 1972 and 1982, with a range of people as set out in Table 3. On each occasion the senior man of the Jampijinpa-Jangala estate, designated number 1 in Table 3, was present and was the person Peterson was referred to for granting permission to visit the mine. However, on the first visit, the senior man (designated number 7) of the adjacent Jupurrula-Jakamarra estate was present, as were also 1's principal *kurdungurlu* ('managers' - designated 5 and 6). On the second visit 7 was not present but an influential man (8) of a Jupurrula-Jakamarra estate, some way to the north of the mine, was custodian (*kirda*) of the section of the widely important kangaroo dreaming track that crosses the Jampijinpa-Jangala estate in the north-south direction a few kilometres to the west of the mine. This man asserted that appropriate Jupurrula-Jakamarra people could hold ceremonies for the mine site. On the third visit, organised at short notice, 1 was again present with two other principal *kurdungurlu*: 12 the actual brother of 5, and 10 his actual father's sister's son.

Hiatt (1982: 24–25) has recently pointed out that monopolization of resources was rare in hunter-gatherer societies, and in Australia applies mainly to those that are scarce, valued and have some durability such as the products of quarries or pituri groves. It seems evident in the case of this mine that there is some competition to exercise control over access, although this is muted. Outright control is complicated by the very close relationships and obligations between those involved. Because 1, 2 and 10 are coresident on the Jampijinpa-

Jangala estate close to the mine they are in a *de facto* position to exercise a control, as all recognise they have a legitimate interest in the mine. Neither 1 nor 2 has ever claimed to us to be able to hold the ceremonies for the site. It was 8 who asserted the rites for the mine were Jupurrula-Jakamarra when 1 was present, although 8 himself did not claim to be the appropriate person to perform them. Nevertheless he did claim that it was his section that controlled the mine, and was not contradicted. At the time, 1 and 2 were indebted to 8 because they were living off a ritually important soakage on his dreaming track, although the general area around the soak was the two brothers' own estate. They were waiting for a bore to be drilled and equipped a little to the south and unequivocally on their own land: this they now have. 7, who seems to be the appropriate Jupurrula-Jakamarra estate owner to exercise control, since his country is adjacent to the mine, on the east, is not an influential man, is without other adult male members of his estate group and spends much of his time in Yuendumu so he is not in a strong position to unilaterally assert his rights. However, as the actual wife's mother's brother of 1, he is obviously in a position of some potential influence.

Thus, while there is some uncertainty over the control of access to the mine, it still remains very much a 'family' affair.

It might be that, as a highly valued but also highly localised resource, there has been an attempt to prevent too localised a monopoly by asserting a broader moiety interest, as the mythology suggests with its intersection of the Jupurrula man dreaming and the Jampijinpa-Jangala rain dreaming. The presence of the women further confirms this. Since nobody claims the deposit to be Jungarrayi-Japaljarri it would seem that an interpretation for the involvement of women of these two subsections might be, following Warlpiri aetiology, that the deposits have been created by the husbands through the agency of their, initially, prepubertal wives. As Jakamarra men are husbands to Napaljarri women, and Jangala men are husbands to Nungarrayi women the deposit would thus belong to both sections of the moiety. But just as the ambiguity of the mythology may prevent monopolization, it also opens the way for it to emerge. If demographic and social factors lead to the demise of one of the patrilines, the way is open for the other to assert control, strengthened today by the very practical consideration of residence on the spot.

It is not entirely clear what advantage accrues to those in control, except and perhaps crucially, an increase in those indebted to them, and a locally intensified rate of circuation of wealth with its concomitant of social centrality. Today, this counts for less as the people live on the geographic fringes of Warlpiri settlement, although access by car may compensate for this to some degree. It is possible that proselytization by the local fundamentalist missionary could inhibit the final assertion of rights involved in performing the ceremony for the site by 1 and 2 and leave the situation as it is. On the other hand, commoditisation may only be round the corner, although curiously it has not yet emerged, in which case the competition for control may intensify.

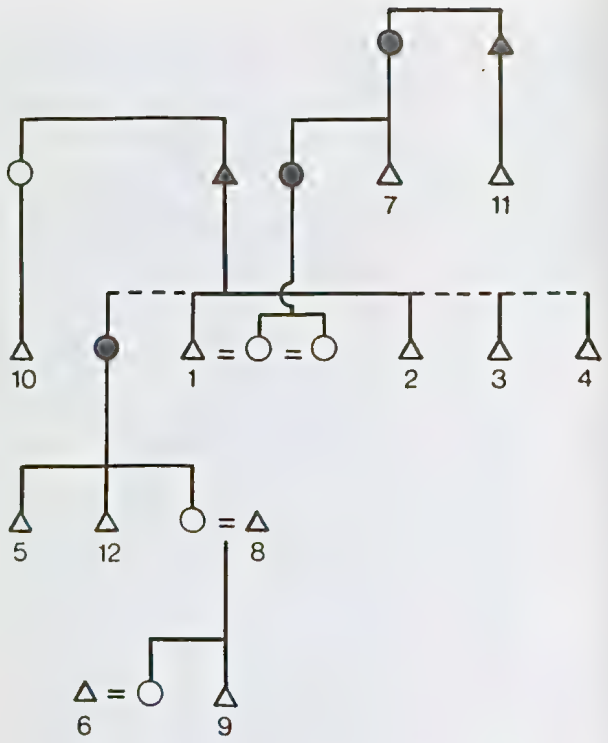


Table 3. Genealogical relationships between Aboriginal members of three parties to the mine. Party one: 1, 2, 3, 4, 5, 6, 7. Party two: 1, 8, 9, 10, 11. Party three: 1, 2, 10, 12. The subsection affiliations are: Jampijinpa: 1, 2, 3, 4; Jupurrula: 7, 8; Jakamarra: 9; Japaljarri: 6, 10; Jungarrayi: 11; Japanangka: 5, 12.

NOTES AND ACKNOWLEDGEMENTS. We would like to record our thanks to the Warlpiri men who took us to their mine and have allowed us to publish this information. It will be noted that we have not located the mine precisely. This is in order to ensure that control over access to it remains in the hands of those entitled to exercise it by Aboriginal tradition. We have had some misgivings about publishing information on this mine before now for fear it might precipitate unauthorised visits or a rush of unwanted visitors. Now the mine is Aboriginal land, formal permission to visit has to be sought, and illegal visitors are liable to prosecution.

We would also like to thank David Nash, Dick Kimber, Les Hiatt, Sandra Bowdler, Francoise Dussart and Eric Michaels for their helpful comments; Luise Hercus for the linguistic information and Rosemary Buchan of the Aboriginal Heritage Unit, Adelaide, for supplying published and unpublished material on the Bookatoo mine.

¡Although this mine is often referred to as the Parachilna mine, Parachilna is, in fact, the name of the Hundred in which it is located. Bookatoo is, apparently, the Aboriginal name for the deposit. There are various spellings of this name; that used in the body of the paper being the one under which the site is registered by the Heritage Unit. Whilst on the matter of spelling it should be mentioned that Wilga mia is also spelt Wilgie mia in some sources.

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Systematics of the Reduce-limbed and Limbless Skinks Currently Assigned to the Genus *Anomalopus* (Lacertilia: Scincidae)

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ABSTRACT. The genus *Anomalopus*, as currently recognized, harbours many of the reduce-limbed and limbless skinks of eastern Australia. In this paper the genus is argued to be polyphyletic and, on the basis of shared derived character states, is subdivided into three genera, one with two subgenera. The taxa are: *Anomalopus* (*Anomalopus*) *mackayi* n. sp., *A.(A.) verreauxii* Duméril & Duméril, 1851 and *A.(A.) leuckartii* Weinland, 1862; *Anomalopus* (*Vermiseps*) *swansoni* n. subgen., n. sp., *A.(V.) pluto* Ingram, 1977, *A.(V.) gowi* n. sp. and *A.(V.) brevicollis* n. sp.; *Ophioscincus truncatus* Peters, 1876, *O. ophioscincus* Peters, 1873 and *O. cooloolensis* n. sp.; *Coeranoscincus reticulatus* Günther, 1873 and *C. frontalis* De Vis, 1888. Data on distribution, habitats, habits and mode of reproduction are given for all taxa as available, and inter- and intrageneric relationships are discussed. Morphological trends within each genus or subgenus are discussed. Keys are provided to the genera of reduce-limbed skinks of Australia and the limbless lygosomines of the world.

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KEYWORDS: Australia, Scincidae, limbless, lizards.

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Skinks are renowned for the frequency with which they undergo limb reduction and loss. If one takes as the end point of this process the total absence of any external trace of limbs, then non-scincid lizards (three-quarters of all lizard species) have lost the limbs (on a very conservative estimate) at least three or four times whereas skinks (about one-quarter of all lizard species) have lost them at least thirteen times. Within skinks the loss has not been uniform across major taxonomic groups. The scincines, acontines and feylinines together account for about one-fourth of all skink species and have lost their limbs at least eight times, whereas the lygosomines, accounting for three-fourths of the species, have lost them at least five times (once in the Asian genus *Isopachys* and once each in the Australian genera *Anomalopus* (s.s.), *Coeranoscincus*, *Lerista* and *Ophioscincus*).

The number of limbless lygosomine species described and recognized as valid to date is eight. However, for several years four additional species, all from eastern Australia, have been known but undescribed. All of these have either been formally or informally assigned to the genus *Anomalopus* (see Cogger, 1973, for first use of the current generic concept), a member of the *Sphenomorphus* group of lygosomines (Greer, 1979). This genus also contains one informally recognised but undescribed reduce-limbed species. The primary purpose of this paper is to describe these five new species and to review their morphology and relationships, and hence make them more readily available to other studies, especially those concerned with limb reduction and loss. Furthermore, as the current diagnosis of *Anomalopus* comes very close to 'all those greatly reduce-limbed Australian skinks with no clear affinities elsewhere', a second, but related, purpose of the paper is to test the monophyly of the group. Finally, to facilitate the identification of reduce-limbed skink genera in Australia and limbless lygosomine species worldwide, keys are presented to both groups.

Materials and Methods

The specimens examined in this study comprise most of the Australian material and much of the overseas material. These have been studied as intact specimens in alcohol, dried skeletons, cleared (KOH and trypsin) and stained (alcian and alizarin) specimens and from X-rays.

Non-obvious head scale designations are given on figures of relatively primitive representatives of each genus and subgenus (Figs 2, 10, 24 and 35). Paravertebral scales are counted in a single row starting from the first scale, in either row, that falls completely beyond an imaginary line drawn along the posterior edges of the thighs, extended at right angles to the body and ending at and including the scale bordering the parietal. In limbless species the count begins with the paravertebral at the level of the anterior edge of the enlarged preanals, a level equivalent to that in limbed species. The digits of reduce-limbed forms are given sequence numbers on the basis of their inferred homologies.

Measurements of the head, body and appendages were made by adpressing the part against a stationary steel rule graduated in 0.5 mm. Measurements of scales were made with an ocular micrometer. Proportions were based on maximum widths and midline lengths. Tail lengths were based on complete tails as determined from X-rays. Brood sizes were determined by dissection of gravid females.

All diagnoses of supraspecific taxa are written for the hypothetical ancestor of the taxon, i.e., they represent the suite of the most conservative derived character states displayed within the taxon *vis a vis* the *Sphenomorphus* group. Descriptions of external morphology for the new species include details of all characters currently recognized as potentially useful in the alpha taxonomy of lygosomines. Descriptions of skeletal characters for all species are limited to characters that either vary intraspecifically or are useful in inferring relationships.

Species synonymies follow Cogger *et al.* (1983).

Descriptive, institutional and statistical abbreviations that are not obvious are as follows:

AM	Australian Museum, Sydney
AMNH	American Museum of Natural History, New York
ANWC	Australian National Wildlife Collection, Canberra
BMNH	British Museum (Natural History), London
CAS	California Academy of Sciences, San Francisco
FMNH	Field Museum of Natural History, Chicago
GZM	Giessener Zoologischen Museum, Giessener, Germany
MNHN	Muséum National d'Histoire Naturelle, Paris
MCG	Museo Civico di Storia Naturale di Genova 'Giacomo Doria', Genova
MCZ	Museum of Comparative Zoology, Cambridge, Massachusetts
MV	Museum of Victoria, Melbourne
QM	Queensland Museum, Brisbane
QNPWS	Queensland National Parks and Wildlife Service, Townsville, Queensland
SAM	South Australian Museum, Adelaide
SD	standard deviation
SVL	snout-vent length
WAM	Western Australian Museum, Perth

$\bar{x}$	statistical mean
ZMA	Zoologisch Museum, Amsterdam
ZMB	Zoologisches Museum, Berlin
*,**,***	significance levels for statistical tests of 0.05, 0.01 and 0.001, respectively

Anomalopus — Is It a Monophyletic Group?

If one accepts that monophyletic taxa should be based on derived character states, then *Anomalopus*, as it is currently construed, shows the following suite of character states that are derived *vis a vis* the *Sphenomorphus* group (Greer, 1979).

Nasal slightly enlarged; prefrontals separated; supralabials six, fourth subocular; external ear opening absent. Rostral, nasal, first supralabial and first infralabial with slightly thickened, milky-coloured epidermis.

Pre- and postfrontal bones approach each other closely above orbit; fenestra rotunda reduced to vertical oval or slit; pterygoid teeth absent; quadratal conch reduced to low ridge or absent; presacral vertebrae $\geqslant$ 43; sternal ribs $\leqslant$ 2.

Manus lacks distal carpals 1 and 5 and metacarpal 1, and has phalanges reduced to 0.2.3.3.0; pes lacks metatarsal 1 and has phalanges reduced to 0.2.3.3.0.

This is a relatively long list of character states and hence is likely to inspire confidence in the concept of *Anomalopus* as a monophyletic group. However, there is a problem in that it is a list of character states that are commonly associated with burrowing. This raises the possibility that the group is a grade of burrowers and not a clade. How is this issue to be resolved, especially when it is not unreasonable to expect burrowers to have other burrowers as their nearest relatives?

Our solution has been to weight characters, specifically to emphasize those characters that do not seem to be part of the suite of modifications regularly seen in burrowers (see pp. 13, 33 and 41). In adopting this approach we are relying on our extensive experience with all the burrowing lineages of skinks and our resultant belief that convergence is widespread within the group.

This approach has led to the conclusion that there are three monophyletic, generic-level taxa within the current concept of *Anomalopus* and that one of these, *Anomalopus* (s.s.), is probably more closely related to a group outside *Anomalopus* (s.l.) than to one within, and that the relationships of the other two taxa, *Ophioscincus* new genus and *Coeranoscincus*, while for the present obscure, are by no means necessarily with each other.

Hence the answer to the question posed above is that *Anomalopus*, as it has been construed to date, is probably not a clade of burrowers but rather a grade.

Genus *Anomalopus* Duméril & Duméril

Anomalopus A.M.C. Duméril & A. Duméril, 1851: 185. Type-species: *Anomalopus verreauxii* A.M.C. Duméril & A. Duméril, by monotypy.

Anomalpus Günther, 1875: 14 (lapsus for *Anomalopus*).

Diagnosis. *Anomalopus* differs from all other members of the *Sphenomorphus* group in the following combination of derived character states: prefrontals separated; last 2 supraoculars partially separated by a superciliary (usually the sixth); supralabials 6, fourth (or suture between fourth and fifth) below centre of eye; external ear opening absent; front and rear limb $\leqslant$ 0.07 x and $\leqslant$ 0.09 x SVL, respectively.

Premaxillary teeth $\leqslant$ 7; ectopterygoid process present; postorbital absent; quadratal conch absent.

Manus lacks distal carpals 1 and 5, metacarpal 1, and has phalanges reduced to 0.2.3.2.0; pes lacks metatarsal 1 and has phalanges reduced to 0.2.2.0.0; presacral vertebrae $\geqslant$ 47; sternal ribs $\leqslant$ 2; medial ends of ischia separated.

Comments. This genus brings together all those *Sphenomorphus* group species that, in addition to having the '*Anomalopus*' suite of burrowing modifications, also show the following not so obviously burrowing-associated features: last two supraoculars partially separated by a supraciliary; premaxillary teeth $\leqslant$ 7; ectopterygoid process present; postorbital absent.

Subgenera. *Anomalopus* Duméril & Duméril comprising the limbed forms, and *Vermiseps* n. subgen. comprising the limbless forms.

Species (7). Subgenus *Anomalopus*: *A. leuckartii* Weinland, 1862; *A. mackayi* n. sp.; and *A. verreauxii* Duméril & Duméril, 1851. Subgenus *Vermiseps*: *A. brevicollis* n. sp.; *A. gowi* n. sp.; *A. pluto* Ingram, 1977; and *A. swansoni* n. sp.

Distribution. Eastern Australia from Cape York Peninsula to central New South Wales (Figs 3,8,12).

Habitat and habits. Low closed forest (vine thicket) through open forest and woodland (various types) to open heath; apparently only rarely in tall closed forest (rainforest) and then generally in openings and clearings. Cryptozoic; generally found under surface cover.

Reproduction. Oviparous (three species) and ovoviviparous (one species). The only known ovoviviparous species (*A. swansoni*) is also the most southern, providing yet another example of the association of this mode of reproduction with life in cooler climates.

Relationships. *Anomalopus* shares three of its four non-burrowing derived character states with the genus *Lerista*, and it would share all four if the failure of the last two supraoculars to be separated partially by a supraciliary were secondarily derived instead of primitive in *L. microtis*. *Lerista* is a large genus, widespread in the arid, semi-arid and seasonally dry parts of Australia, with its most primitive members in the temperate zone (pers. obs.). *Anomalopus*, as represented by the most primitive species in each of its two subgenera, *A. mackayi* in *Anomalopus* and *A. swansoni* in *Vermiseps*, is similar to *Lerista* in being

distributed in relatively open habitats (e.g. woodland) and in having its most primitive species restricted to the temperate zone.

Key to Species of Anomalopus

1. Limbs present.....subgenus *Anomalopus*...2
——Limbs absent.....subgenus *Vermiseps*...4
2. Three toes on front limb.....3
——Two toes on front limb.....*A.(A.) leuckartii*
3. Two toes on rear limb.....*A.(A.) mackayi*
——Styliform rear limb.....*A.(A.) verreauxii*
4. Nasals separated (rarely in contact in *A. swansoni*); prefrontals present.....5
——Nasals in contact; prefrontals absent.....6
5. Nasal extends to lip (through fusion with 'first' supralabial?).....*A.(V.) pluto*
——Nasal separated from lip by first supralabial.....*A.(V.) swansoni*
6. Supraoculars usually 3 (84%), occasionally 2 (16%); frontoparietals meet; supralabials 6; paravertebrals 86–102.....*A.(V.) brevicollis*
——Supraoculars 2; frontoparietals usually separate (89%); supralabials usually 5 (90%), occasionally 6 (10%); paravertebrals 108–116.....*A.(V.) gowi*

Subgenus *Anomalopus* Duméril & Duméril

Type-species. As for genus.

Diagnosis. There are three derived character states that will diagnose this group as a distinct lineage *vis a vis* the subgenus *Vermiseps*: larger size (maximum SVL of smallest species = 123 mm vs maximum SVL of largest species of *Vermiseps* = 108 mm), dedifferentiation of the transversely enlarged nuchal scales (mode = 0), and reduction of fenestra rotunda to a small foramen. For purposes of rapid identification it may be distinguished from this group by the retention of limbs.

Species (3). *Anomalopus leuckartii* Weinland, 1862; *A. mackayi* n. sp.; and *A. verreauxii* Duméril & Duméril, 1851.

Distribution. Central eastern Australia from southeast Queensland to central eastern New South Wales (Figs 3,8).

Habitat and habits. Closed and open forests, woodlands and open paddocks. Generally found under cover (rocks and logs) over loose or semi-consolidated substrates; generally tries to escape by undulating/crawling laterally into the surface litter instead of diving into the substrate.

Reproduction. Oviparous (two species).

***Anomalopus mackayi* n. sp.**

Figs 1–2

Type-material. HOLOTYPE. Australian Museum R 3834: Eurora, Walgett, N.S.W.; collected by 'Mr. Raven' and presented to the museum by C.N. Vaughan; no date of collection available; male.

PARATYPES. AM R 2383: locality unknown; R 3834, 13138: Old Burren, N.S.W.; R 14007: Gnoumery Station, Goodooga, N.S.W.; R 16902: Burren Junction, N.S.W.; R 17712, 21006: Bellata, N.S.W.; R 69665: Culgoora, N.S.W.

FMNH 73852: Wee Waa, N.S.W.; 75142, 75144: locality unknown.

QM J 8516: Allora, Qld; J 42433: Bongeen area, 20 km S of Cecil Plains, Qld; J 42531: 24 km NNW of Oakey (by road), Qld.

Diagnosis. Differs from all other *Anomalopus* and indeed all other lygosomines in having a digital formula of 3–2.

Description. A moderately long, attenuate skink with small front and rear limbs and a plain brown colour pattern.

Snout bluntly rounded; rostral with broad, moderately deep median lobe projecting between nasals to make narrow contact with frontonasals; frontonasal wider than long (1.4–1.8 x); prefrontals well developed but widely separated; frontal slightly longer than wide (1.2–1.4 x) and slightly shorter than midline length of frontoparietals and interparietal; supraoculars 4, first 2 in contact with frontal; frontoparietals paired, in contact, each shorter and broader than interparietal; interparietal distinct, with distinct parietal eye spot; parietals meet behind interparietal; each parietal bordered posterolaterally by large upper secondary temporal and 2 to 3 more-or-less equally sized body scales; transversely enlarged nuchals 0–1.

Nasals large and separated, nostril situated slightly forward and below centre point; loreals 2,

Fig. 1. *Anomalopus mackayi* n. sp. from 24 km NNW of Oakey (by road), Qld. Photo: A.E. Greer.

approximately equal in size and proportions; preoculars 2, lower much the larger; supraciliaries 6 to 7, first separated from frontal, penultimate occasionally projects slightly medially between third and fourth supraoculars, and ultimate projects medially between last supraocular and pretemporals; suboculars large and forming a continuous row comprised of 1 presubocular, 2 suboculars and 1 postocular; lower eyelid scaly; pretemporals 2; primary temporal single; secondary temporals 2, upper very long and overlapping lower which is about equal in size to primary temporal; tertiary temporal single; external ear opening absent, represented by an anteriorly dipping, shallow auricular crease; supralabials 6 or 7, fourth smallest and situated directly below centre of eye; postsupralabials 2; infralabials 6 or 5; mental large, wider than long (1.7–2.3 x); postmental much wider than long, in contact with first two infralabials on each side; enlarged pairs of chin scales 3, first in contact, second separated by 1 scale row and third separated by 3.

Body scales smooth, in 18–20 longitudinal rows at midbody; paravertebral scales only slightly wider than those in more lateral rows, 97–116 in a single row; inner preanals overlap outer, medial pair enlarged; median row or subcaudals equal in size to immediately adjacent rows.

Snout-vent length 63–123 mm; front leg with 3 very short, clawed toes of which middle is longest, 0.05–0.07 x SVL; rear leg with 2 very short clawed toes of which second is longer, 0.04–0.08 x SVL; tail pointed, 1.03–1.21 x SVL.

Presacral vertebrae 51–58; complete inscriptional chevrons 11–13; sternal/mesosternal ribs 2/2.

Manus comprises radiale, ulnare and pisiform (intermedium could not be assessed); centrale; distal carpals 2–4; metacarpals 2–5, and phalanges 0.2.3.2.0.

Pes comprises fused astragalus and calcaneum; distal tarsals 3–4; metatarsals 2–5; phalanges 0.2.2.0.0.

Colour. In preservative the ground colour of the dorsum ranges from light, greyish brown to dark-brown

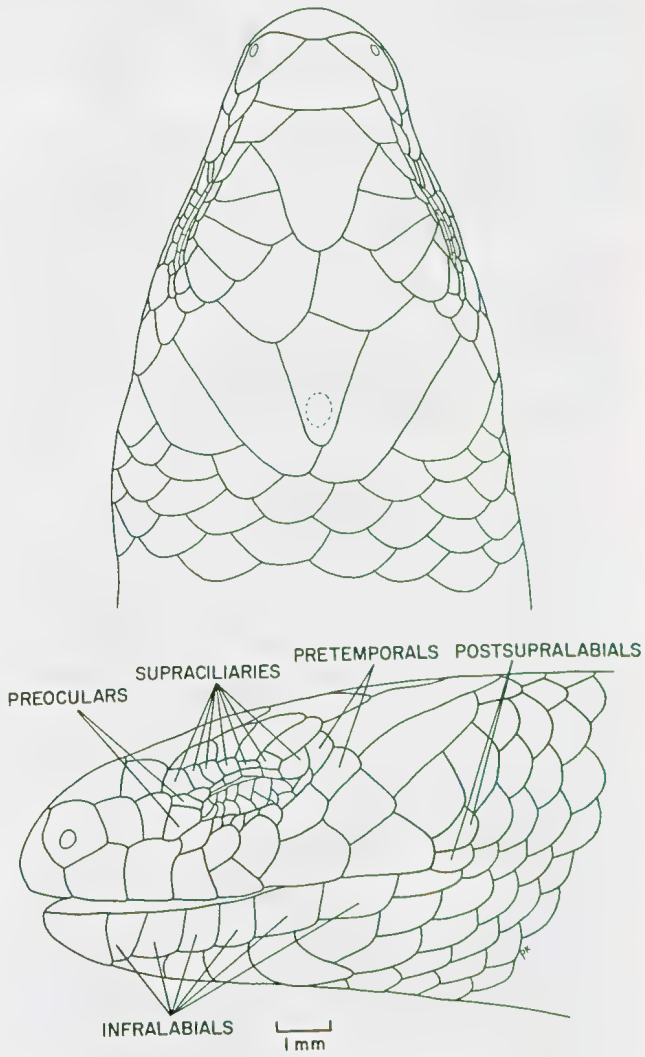

Fig. 2. Head of *Anomalopus mackayi* n. sp. (AM R 3834; holotype) with certain head scales labelled.

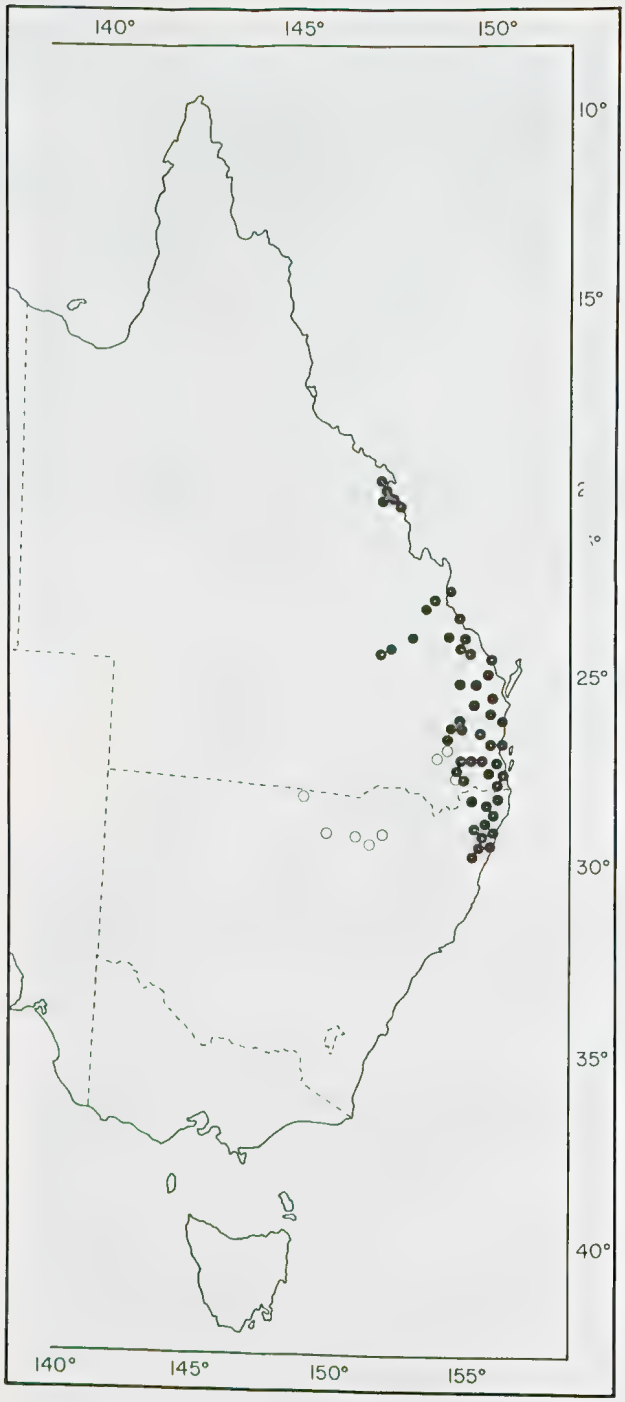

Fig. 3. Distribution of *Anomalopus mackayi* (open circles) and *A. verreauxii* (closed circles) (See addendum).

and the venter from off-white to light-brown. The dorsal pattern is uniform in New South Wales specimens but consists of rows of dark-brown dots or dashes through the centres of the dorsal and lateral scales in the Queensland specimens. The venters are unpatterned in most specimens but consists of rows of dark spots like the dorsum in one Queensland specimen (QM J 8516).

Details of holotype. The holotype (AM R 3834; Fig. 2) has 7 supralabials on left side and 6 on right; 18 midbody scale rows; 104 paravertebral scales; SVL 110 mm, and tail regenerated.

Etymology. Named for Roy D. Mackay, formerly of the Australian Museum and founder of the Australian Herpetological Society.

Distribution. The 12 specimens of *A. mackayi* with locality data are from a relatively small area just west of the Dividing Range in northeastern New South Wales and southeastern Queensland
(Fig. 3).

Habitat, habits and reproduction. Nothing known. of the
Australian

lopus verreauxii Duméril & Duméril

Distributio Figs 4–5
locality data a
of the Dividing*reauxii* A.M.C. Duméril & A. Duméril, 1851: and southeastcality: Tasmania (in error). Holotype: MNHN (Fig. 3).

Habita–ope, 1864: 229. Type-locality: Australia. Type(s): ...known.

Anomalopus Godeffroyi Peters, 1867: 24. Type-locality: east Australia. Syntypes: ZMB 5296–7.

Chelomeles pseudopus Günther, 1873: 145. Type-locality: unknown. Holotype: BMNH 1946.8.3.59.

Material examined. Localities have been omitted for this common and widespread species in order to save space (Fig. 3).

AM R 587, 3973, 4051, 5319, 5525–27, 5531, 6437–40, 8534, 9458, 10019, 11385, 11683, 12868, 13397, 13764, 13836, 14817, 18279–80, 18285, 18290–92, 18294–95, 21127, 21370, 24684, 26616, 27994, 33035, 40291, 47484, 48099, 51693, 54612, 54618, 55020, 55065, 65908, 66290–91, 66293–316, 67161, 76133–37, 76144–46, 76229, 89271–72, 93770, 110619–20, 110638–39, 110641–42, 111364–68, 111414, 114040–46, 114092, 115670–73.

MV D 550–51, 589, 593, 596–97, 1056–57, 4190–91, 4197–99, 10251, 15293–15296, 42598, 53595.

QM J 140, 153, 170, 214, 223, 360, 363, 383, 472, 499–501, 1279, 1472, 1504, 1519, 1547–80, 1834, 1903, 2052–53, 2419, 2440–41, 2561, 2859, 3020, 3048, 3136, 3422, 3431, 3467, 3469, 3518, 3564, 4086, 4194, 4424, 4753, 4791, 4997, 5770, 6061, 6777, 6861, 7075, 7227, 7300, 7370, 7392, 7424, 7466, 7763, 7913, 7935, 8172, 8310, 8385, 8515–16, 8536, 8544, 8609, 8618, 8658, 8662–63, 8694, 8711–12, 8841, 9034, 9039, 9107, 9124, 9264, 9269–70, 9603, 9727–28, 9760, 9901, 9910, 9938, 10299, 10441, 11095, 11099, 11114, 11574, 11621, 11827–40, 12244, 12248–50, 13556, 13683–84, 15286, 15681, 15743, 16954, 20133, 21018, 22014, 22022, 22027, 22289–90, 22356, 22968, 24039, 27525, 33639–40, 35709–10, 36105, 36929–30, 37065, 38525, 40128, 41961.

QNPWS N 2024, 10892.

SAM 3931.

Diagnosis. This is the only species of *Anomalopus*, and indeed lygosomine, with the digital formula 3–1, the front leg bearing three very short, clawed toes and the rear leg represented by a clawless nubbin.

Description. *Anomalopus verreauxii* is very similar to *A. mackayi* in most regards, and hence may be most usefully described in comparison to this species (also see Table 1).

Rostral slightly larger and projecting more dorsally,

Fig. 4. *Anomalopus verreauxii* from approximately 4.2 km SW of Maleny, Qld. Photo: A.E. Greer.

hence frontonasal shorter and broader; supraoculars generally 4, but occasionally reduced to 3, first two always in contact with frontal; transversely enlarged nuchals 0–2.

Nasal slightly larger, nostril situated slightly forward of centre; infralabials 5; mental slightly larger and extending more posteriorly, hence shorter and broader overall; paravertebral scales more numerous, 110–129; snout-vent length appreciably greater, 44–185 mm; front and rear legs relatively shorter (0.03–0.06 and 0.01–0.03 x SVL, respectively); rear leg styliform, clawless.

Presacral vertebrae 53–57; postsacral vertebrae 57–62; complete inscriptional chevrons 12–14; sternal/mesosternal ribs 3/2–2/2.

Manus comprises radiale, intermedium (sometimes absent), ulnare and pisiform; centrale; distal carpals 2–5; metacarpals 2–5, and phalanges 0.1.2.2.0 (basal 2 phalanges may fuse in digits 3–4 in older specimens).

Pes comprises astragalus and calcaneum, distal carpals 3–4 and metatarsals 3–4.

Colour. In preservative, *A. verreauxii* is generally uniformly brown to dark-grey above and off-white to pale 'dirty' brown below; a light nuchal collar is very distinct in juveniles but becomes suffused with pigment in adults. In life, the nuchal collar and venter of the chin, throat and anterior body may be various shades of yellow (Fig. 4; see McPhee 1979, plate 50, for colour photograph of live specimen).

Distribution. *Anomalopus verreauxii* ranges along the east coast from the vicinity of Proserpine, Qld, south to Red Rocks, N.S.W. (Fig. 3). Despite its widespread distribution on the coast it is apparently known from only two islands: Great Keppel (MV D 42598) and Bribie (QM J 3422). The most inland locality which can be reliably accepted is Palm Gorge Fauna Reserve, Qld (QM J 37065) approximately 225 km from the coast. In the north, the range roughly coincides with the arid corridor that comes to the coast between Bowen and Townsville while in the south, it appears to coincide with the southern edge of the Clarence Basin.

Three localities associated with museum specimens have been omitted from the distribution map (Fig. 3) due to the fact that they are well outside the range as determined from more-or-less contiguous records. These are Wyong, N.S.W. (SAM 3931), 6.4 km W of Armidale (AM R 51693) and Charleville, Qld (QM J 1553).

Variation. Occasional specimens of *A. verreauxii* have a reduced number of digits on the front foot that appears to be due to normal variation instead of disease or injury. These are as follows: QM J 11831 — locality uncertain: 2 toes on left front foot, 3 on right (2–3); QM J 11837 — 32 km N of Dayboro, Qld: 2–2; QM J 22289–90 — Bulburin Forest Camp, Qld: 2–3 and 3–2, respectively and AM R 33035 — Rockhampton district, Qld: 2–2. QM J 11831 and J 22289–90 are reliably assigned to *A. verreauxii* on the basis of their having three toes on at least one front foot, and large size (SVL = 170, 176 and 182 mm, respectively vs a maximum of 137 mm for *A. leuckartii*), and J 22289–90 at least came from a population known to include three-toed animals. QM J 11837 is probably an *A. verreauxii* on the basis of its occurence well within the range of this species (and far from the nearest *A. leuckartii*) and the fact that it was taken with a three-toed specimen (QM J 11836). AM R 33035 is assigned to *A. verreauxii* on the basis of its large size (SVL = 143 mm), but it could be interpreted as an exceptionally large *A. leuckartii*.

A light nuchal collar, albeit only faintly expressed in some large specimens, has been found in every specimen

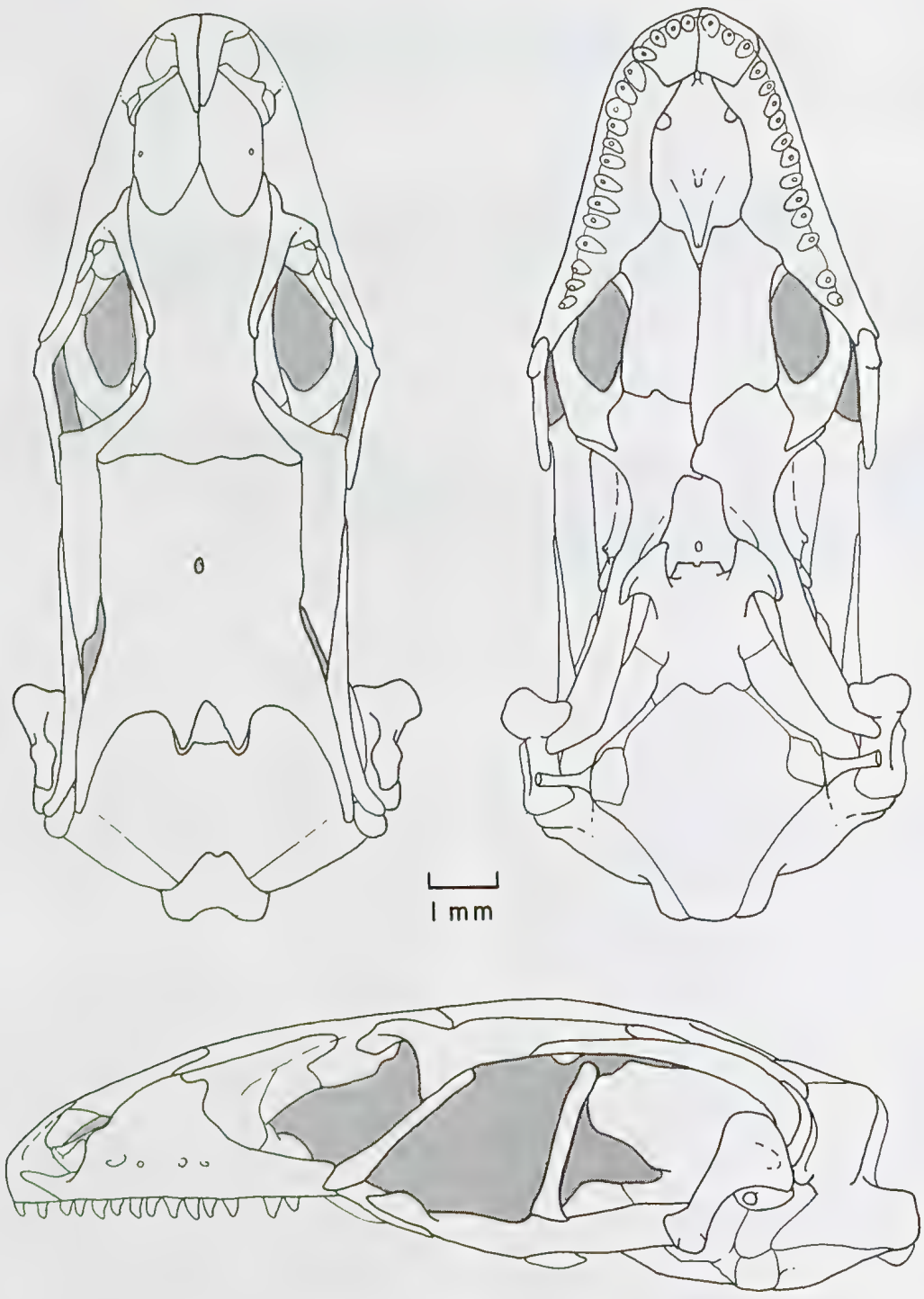

Fig. 5. Skull of *Anomalopus verreauxii* (AM R 6437).

examined for the trait (N = 115) except one: AM R 114092 from Mount Morgan. This specimen is especially significant because it is a juvenile, and in such young specimens the nuchal collar is usually very sharp.

Habitat. *Anomalopus verreauxii* occurs in habitats ranging from large man-made clearings through dry sclerophyll forest and woodland to closed forest (where it is most often found in openings and clearings). The species has been collected at three sites in the Australian Museum and Queensland Museum's joint faunal survey of eastern Australian rainforests (Anonymous, 1976; Broadbent & Clark, 1976; and Covacevich, 1977). At Bulburin State Forest it was found in wet complex notophyll vine forest (adjacent to site 1) and moist low

microphyll vine forest (adjacent to site 3). *Ophioscincus ophioscincus* was also found in the same habitats at both sites. *Anomalopus verreauxii* has also been taken at Marlaybrook in the Bunya Mountains (site 57). This is a semi-evergreen vine thicket with *Brachychiton*.

Habits. Cryptozoic, generally found under surface cover, e.g. rocks, logs and debris; 'commonly discovered under piles of rubbish in many of the suburbs of Brisbane' (Dale, 1973).

Longman (1916) notes that 'when a living *L.*[*Lygosoma*] *verreauxii* is placed on the ground, the stumps are moved with remarkable speed and vigor in the endeavour to promote locomotion over a comparatively smooth surface'.

In small specimens the claws of the front foot are usually relatively long and sharply pointed; however, in larger specimens the claws are often worn down, sometimes to skin level (pers. obs.).

Reproduction. Oviparous (Dale, 1973). We have found five gravid female *A. verreauxii* in the collections examined. All are from southeastern Queensland. One of these contains 11 very large ovarian eggs or recently ovulated oviducal eggs, and the other four contained 3–11 shelled oviducal eggs. Snout-vent lengths of the four measurable specimens range 128–182 mm and the two available dates of collection are 6 and 12 November. S.J. Copland reports (field notes for S.J.C. 3812–17) finding a clutch of six eggs at Hortons Creek, N.S.W., which hatched in the period 11–13 March.

Taxonomic comments. The following species have been assigned to the synonymy primarily on the basis of the unique (to lygosomines) digital formula of 3/1.

The type of '*S. simplex*' Cope, 1864, has not been found (Cogger, pers. obs.) but Cope's description of a digital formula of 3/1 and a 'yellowish occipitonuchal collar' can only pertain to *Anomalopus verreauxii* within the Australian herpetofauna. All other parts of Cope's description also accord well with this species.

The two syntypes of *Anomalopus Godeffroyi* Peters, 1867, have not been examined by us, but because Peters himself noted it was distinguished from *A. verreauxii* only by the presence of a scaly eyelid (the eyelid being described as 'transparent' in the original description of the latter), and only provisionally recognized it as a distinct species, we feel confident in relegating *A. Godeffroyi* to the synonymy of *A. verreauxii*.

One of us (H.G.C.) has examined the holotype of *Chelomeles pseudopus* Günther, 1873. Its digital formula of 3/1, light (albeit faint) nuchal collar, lack of an external ear opening, 20 midbody scale rows and large size (SVL ca 189 mm) make it clearly assignable to *Anomalopus verreauxii*.

Anomalopus leuckartii Weinland

Figs 6–7

Brachymeles Leuckartii Weinland, 1862: 140. Type-locality: Australia. Types(2): GZM, lost (fide W. Böhme, pers. com.). Neotype (designated herewith): Australian Museum R 44677, Ironbark Ck, approx. 25 km WSW of Bundarra via Barraba Rd, N.S.W., 11 March 1975, S. Bolin, male.

Anomalopus lentiginosus De Vis, 1888: 823. Type-locality: Brisbane. Type(s): presumably lost (fide Covacevich, 1971).

Lygosoma verreauxii biunguiculata Oudemans, 1894: 145. Type-locality: Burnett R., Qld. Syntypes: ZMA 11398–11399.

Lygosoma bancrofti Longman, 1916: 49. Type-locality: upper Dawson R. district, Qld. Holotype: QM J 2560.

Lygosoma verreauxii biungulata Zietz, 1920: 219. Lapsus for *Lygosoma verreauxii biunguiculata* Oudemans, 1894.

Lygosoma bankrofti Zietz, 1920: 219. Lapsus for *Lygosoma bancrofti* Longman, 1916.

Material examined. Localities have been omitted for this common and widespread species in order to save space (Fig. 8).

AM R 2932, 2934, 2936–38, 3619–20, 4018, 4267, 5336, 5455, 5834, 6118, 6339 A–B, 6350, 6733, 8986, 9017, 9375, 9391, 10378, 13057, 13102, 13753, 14956–58, 15031, 15112, 15575–78, 15664, 15758–59 A–C, 17867, 20369, 21307, 26107–15, 27978, 28639–40, 31784, 33034, 43917–72, 43975–78, 44677, 44684–86, 44695, 44717, 44722, 47479–80, 52992–94, 55071–72, 55665, 62311–13, 62676, 64668, 66292, 66317–18, 67155–60, 68355, 69727, 70563–65, 71320, 73613, 73707–11, 76601–02, 77113, 84932–35, 86929, 89108–09, 89199–200, 91119–22, 92429, 95811, 96414, 96656, 99338, 101339, 102987, 104021, 104315, 104828, 111795, 112851, 115674–75.

MV D 105–08, 595, 50976, 51969–72.

QM J 783, 1567, 2560, 3768, 5408, 9095–99, 13935, 24040–41, 28610, 36968, 37022–23, 42193.

QNPWS N 10534, 10865, 28890–91.

Diagnosis. The only species of *Anomalopus* with the digital formula 2–1, the front leg bearing 2 very short clawed toes and the rear leg represented by a clawless nubbin (clawed on the right side in AM R 47480). Differs from the only other lygosomine with the 2/1 digital formula (*Larutia miodactylus*) in having a complete series of large, subocular scales and more paravertebral scales (108–128 vs 96–103).

Description. Like *A. verreauxii*, *A. leuckartii* is very similar to *A. mackayi* and may be described in terms of its differences with this species (also see Table 1).

Rostral appreciably larger and projecting more dorsally, hence frontonasal shorter and relatively broader; supraoculars 2–4, the first 2 or only the first in contact with frontal; transversely enlarged nuchals 0–4; nasal appreciably larger, nostril situated well forward of centre; anterior loreal appreciably larger than posterior loreal; supraciliaries 6–7 (mode = 6); fourth supralabial invariably situated below centre of eye; infralabials 6; mental much larger, extending more posteriorly, hence postmental shorter and relatively broader; paravertebral scales more numerous 108–128; snout-vent length slightly greater, 39–137 mm; fore and rear legs relatively shorter (0.03–0.04 and 0.01 or less, respectively); forelimb didactyl, inner digit shorter than outer; rear limb styliform, clawless.

Presacral vertebrae 51–55; postsacral vertebrae 50–54; complete inscriptional chevrons 10–14; sternal/mesosternal ribs 2/2–2/1.

Manus comprises radiale, ulnare and pisiform; distal

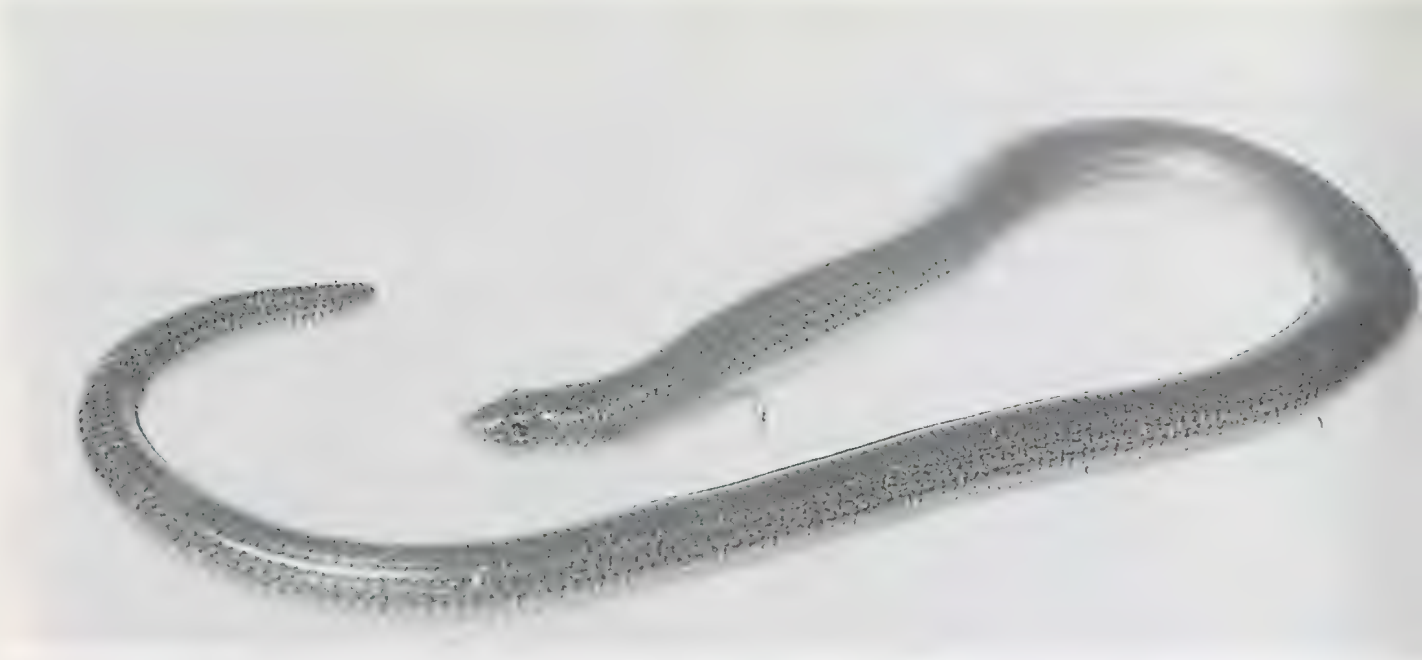

Fig. 6. *Anomalopus leuckartii*. Photo: A.E. Greer.

carpels 2–4, metacarpals 2–4 and phalanges 0.1.2.0.0..

Pes comprises astragalus and calcaneum.

Colour. In preservative, *A. leuckartii* is light-brown to grey-brown dorsally and off-white to pale 'dirty' brown ventrally (Fig.6). A light nuchal collar occurs commonly in Queensland populations (see below); these specimens can be distinguished from similarly patterned *A. verreauxii* by the 2 digits on the front foot, instead of 3, and the relatively shorter hindlimb. In life, the venter of the body may be uniform light-yellow (pers. obs. A.E.G.).

Distribution. *Anomalopus leuckartii* ranges from the Rockhampton district in southeastern Queensland (AM R 33034), south to Muswellbrook (AM R 15758-15759), Kandos (AM R 52992) and Cumnock (AM R 8986) in central eastern New South Wales (Fig.8).

Variation. There is only one specimen that has other than 2 toes on the front foot: AM R 26109 with a single clawed digit on each front foot. The specimen is one of nine from Crows Nest, Qld, and the other eight have 2 clawed toes on each front foot. There is also a single specimen with a claw on each styliform rear limb: AM R 47480 from the Warrumbungle Mountains, N.S.W.

A light nuchal collar — similar to that in *A. verreauxii* — occurs in many populations north of the granite belt in Queensland. The type of *Lygosoma leuckartii* and one of the types of *Lygosoma verreauxii biunguiculata* are specimens from such populations. The nuchal area is uniformly coloured in all southern populations (Fig.6). The species range is greatly constricted at the approximate demarcation point between these two groups (Fig.8).

Habitat and habits. To judge from both the general locality records and the many specific habitat observations for *A. leuckartii*, it appears as if the species is confined almost exclusively to sclerophyll forest and woodland.

Cryptozoic, generally found under surface cover, e.g. rocks and logs.

Respiration involves axillary expansion and contraction (Greer, pers. obs.).

The critical thermal maximum temperature as determined for one specimen was 35.8°C (Greer, 1980).

Reproduction. Oviparous ('embryos removed from eggs': AM R 15759 a–c). We have found four gravid females in collections; three have locality data and are from northeastern New South Wales. The females measure 107, 113, 129 and 134 mm and carry 3, 4, 4 and 4 ovarian (N = 1) or oviducal eggs (N = 3). The specimens with data were collected 25 Nov., 5 Dec. and 6 Dec., respectively.

Taxonomic comments. Species have been assigned to the synonymy of *Anomalopus leuckartii* primarily on the understanding that it is the only Australian species with a digital formula of 2/1. In the following accounts we comment specifically on digital formula and also on the nuchal collar which is variable within the species.

The two syntypes of *Brachymeles Leuckartii* Weinland, 1862, appear to have been destroyed during the World War II (W. Böhme *in litt.*, 10 January and 6 February 1985). However, the type-description is fairly complete and specifically mentions two toes on the front foot and a styliform rear leg. It says nothing about a nuchal collar and hence implies a uniformly coloured nuchal area.

The type(s) of *Anomalopus lentiginosus* De Vis, 1888, are presumably lost (Covacevich, 1971) but the original description mentions a didactyl forelimb and a minute, undivided hindlimb. It also says 'a trace of a pale band across the occipital conspicuous in the young.' The type-locality of Brisbane is odd in that the species does not occur there (G. Czechura, *in litt.*, 10 January 1985). We regard De Vis' specimens as having erroneous locality data, but it is also possible that they were actually *A.*

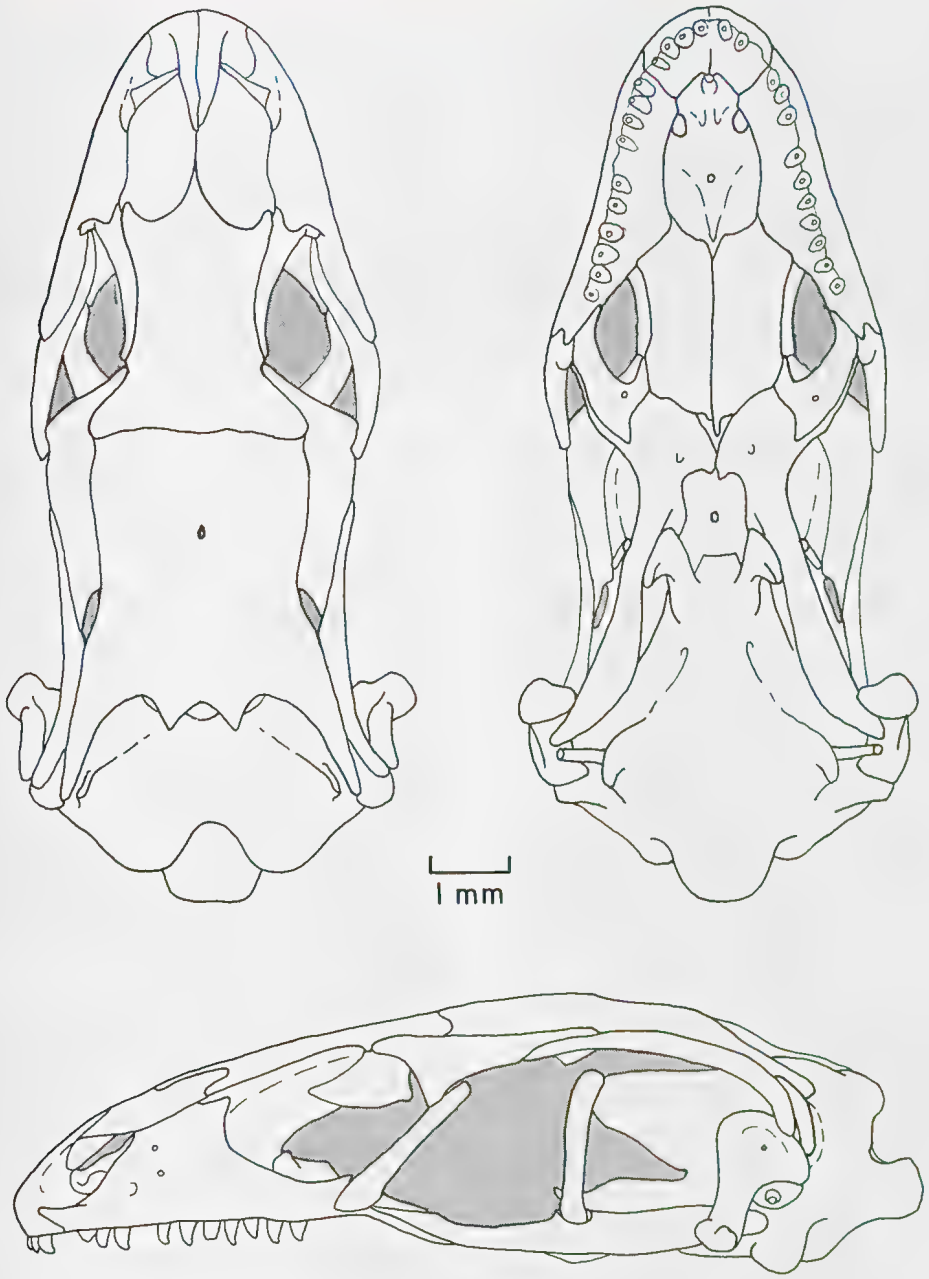

Fig. 7. Skull of *Anomalopus leuckartii* (AM R 43949).

verreauxii with the digits of the forelimb miscounted or truly variable. *Anomalopus verreauxii* is common in the Brisbane area (Dale, 1973; Czechura & Miles, 1983).

Because Weinland's *A. leuckartii* had never once been used as the valid name for this taxon, whereas De Vis' *A. lentiginosus* has frequently been used in the literature, Cogger *et al.*(1983) regarded *Brachymeles Leuckartii* as a *nomen oblitum* and continued to use the long-accepted junior name *A. lentiginosus*, consistent with Article 23 (a–b) of the International Code of Zoological Nomenclature. However, it is clear that with the loss of the types of both species, it becomes important to fix the species long known as *A. lentiginosus* by designation of a neotype. However, as such a neotype could not be consistent with both the locality and the morphology of *A. lentiginosus*, as cited in the original description (see above), we prefer to resurrect the name *A. leuckartii* Weinland, 1862, for this species, and to designate as neotype AM R 44677. This specimen has two toes on the front foot and a styliform hind limb, a uniformly coloured nuchal area, 22 midbody scale rows, 113 paravertebrals, a snout-vent length of 99 mm and a tail length of 114 mm, of which 7 mm is regenerated.

One of us (H.G.C.) has examined the two syntypes of *Lygosoma verreauxii biunguiculata* Oudemans, 1894.

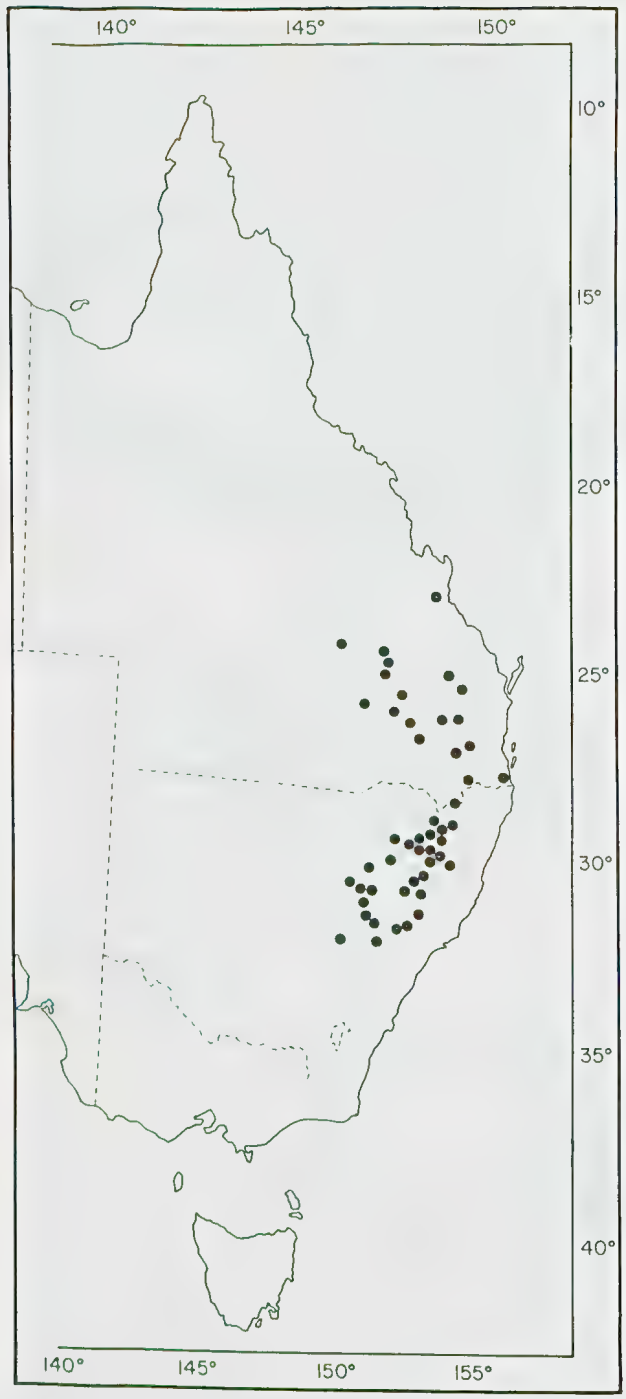

Fig. 8. Distribution of *Anomalopus leuckartii* (See addendum).

Both specimens have a didactyl forelimb and a minute, styliform rear limb. One has uniform dorsal colour and the other a 'distinct lighter zone across the hind edge of the parietals'.

Both of us have examined the holotype of *Lygosoma bancrofti* Longman, 1916. It has a digital formula of 2/1 and uniformly coloured nuchal area.

Morphological Trends and Species Relationships within the Subgenus *Anomalopus*.

Theoretically, one might expect that as the components of limbed locomotion declined in importance, the components of the potentially complementary trunk locomotion (lateral undulation) might increase. Indeed, there are preliminary results and statements in the literature to suggest that such is the case (Sewertzoff, 1931; Presch, 1975; Lande, 1979; Renous & Gasc, 1979). As the three species of the subgenus *Anomalopus* show different degrees of limb reduction, they provide an opportunity to test this relationship.

Within *Anomalopus*, limb reduction, whether it be measured by digit number, total number of limb bones, absolute length or relative length, forms the following transformation series: *A. mackayi* → *A. verreauxii* → *A. leuckartii*. However, segmentation and elongation of the trunk, the former measured by paravertebral scales and presacral vertebrae, and the latter by snout-vent length, form the series: *A. mackayi* → *A. leuckartii* → *A. verreauxii*. Hence the theoretical relationship between limb reduction and trunk elongation and segmentation does not seem to hold. Indeed, it would seem as if the functional significance of trunk segmentation probably has more do to with trunk elongation, i.e. size increase, than limb function. Trunk segmentation may be the method of increasing size, while maintaining the suppleness required for efficient lateral undulation. Size increase in *Anomalopus* may relate to ecology: to judge from general distribution, size increases from xeric (inland) to mesic (near coastal) habitats (Figs 3,8).

The only clear correlation with limb loss in *Anomalopus* is midbody scale row increase. The functional significance of this relationship is obscure.

All the morphological trend data above can be interpreted to support the hypothesis of a close relationship between *A. verreauxii* and *A. leuckartii*.

Vermiseps n. subgen.

Type-species. *Anomalopus* (*Vermiseps*) *swansoni* n. sp.

Diagnosis. Differs from the subgenus *Anomalopus* in the following combination of derived character states: nasals greatly enlarged; supraoculars 3 or fewer, only first in contact with frontal; supraciliaries 4 or fewer; postsupralabial single; tail bluntly rounded; ventral hues lacking.

Pre- and postfrontal bones in contact above orbit; limbs totally lacking.

Etymology. From *vermes* — worm, and *seps* — lizard. The name is meant to draw attention to the limbless, and hence 'worm-like', appearance.

Species (4). *A. brevicollis* n. sp.; *A. gowi* n. sp.; *A. pluto* Ingram, 1977 and *A. swansoni* n. sp.

Distribution. Eastern Australia, from Cape York Peninsula to central New South Wales (Fig. 12).

Fig. 9. *Anomalopus swansoni* n. sp. from Hamilton, Newcastle, N.S.W. Photo: H.G. Cogger.

Habitat and habits. Low, closed forest (vine thicket) and open forest, woodland and open heath.

When uncovered, these skinks almost invariably try to escape by 'swimming' into the substrate.

Reproduction. Oviparous (one species) and ovoviviparous (one species).

Anomalopus swansoni n. sp.

Figs 9–11

Type-material. HOLOTYPE. Australian Museum R 67162: Raymond Terrace area, N.S.W.; R. Wells and R. Cook; 2 December 1973; female.

PARATYPES. All localities are along the central coast of New South Wales.

AM R 6961, 15183, 16433–34, 115676: locality unknown; R 3648: Pitt Town via Windsor; R 4820, 6078: Milson I., Hawkesbury R.; R 4915: Pokolbin; R 9277–8, 107551–53: Raymond Terrace; R 11558, 17921: Newcastle; R 12505, 30290: Merewether; R 13788: Tuggerah; R 13894: Jones Beach, Gosford; R 14355, 67163: Toukley; R 14885, 21040–41, 29962–63, 112413–15: Norah Head; R 15083: Broken Bay; R 21042–44: N.S.W. central coast; R 28552–53: Hamilton, Newcastle; R 32717: The Entrance; R 32718, 57121, 69198, 69204, 71324: Sandy Hollow; R 39009; Muogamarra Nature Reserve, near Berowra; R 49100, 52995: 29 km S of Singleton via Putty Road; R 54282: Waratah, near Newcastle; R 57120: Belmont; R 65236: near Sandy Hollow; R 76612–15: Myall Range; R 89120, 112024: Denman; R 89273–75: 8.1 km S of Bulga PO via Hwy 69; R 98693: Myall National Park; R 106102–04: ca 3 km E of Raymond Terrace; R 106639–40: Little Cattai Ck, 2.0 km N of Cattai.

CAS 94471: near Catherine Hill Bay.

QM J 44236: Sandy Hollow.

Diagnosis. Differs from all other *Anomalopus* in the following combination of characters: limbs totally lacking; supraciliary row complete; loreals 2.

Description. A medium-sized, limbless skink with predominantly light to dark dorsal ground colour but with slight aggregations of pigment in the centre of each dorsal scale giving a punctate or striped pattern.

Rostral trilobed with blunt, round medial lobe projecting partially or completely between nasals to level just posterior to nostril and 2 lateral lobes projecting to same level; frontonasal wider than long (1.6–2.3 x); prefrontals moderate in size, widely separated; frontal slightly wider than long (1.1–1.3 x) supraoculars usually 3, rarely 2, only first in contact with frontal; frontoparietals distinct, in contact, each shorter than interparietal; interparietal distinct with dark parietal eye evident at base of posterior lobe; parietals meet behind interparietal, each bordered posterolaterally by large, upper secondary temporal, nuchal and 2 scales intercalated between; nuchals undifferentiated (i.e., not enlarged).

Nasals greatly enlarged, usually narrowly separated but rarely in contact; nostril situated slightly below and well forward of centre; loreals 2, anterior larger; preoculars 2; supraciliaries 4, in continuous series, first separated from frontal, third interdigitates between second and third supraoculars when these scales distinct; suboculars 4, large, in continuous series and interdigitating with supralabials; lower eyelid movable and scaly; pretemporals 2, first usually not contacted by frontoparietal (86.5%, N = 89) but occasionally so (13.5%); primary temporal single; secondary temporals 2, upper overlaps lower; external ear opening completely covered by scaly epidermis, its former position indicated by shallow vertical depression; supralabials 6, first by far largest, fourth smallest and generally situated below centre of eye, although occasionally suture between third and fourth supralabials subocular; postsupralabial single; infralabials 6, first 2 in contact with postmental; mental large, wider than long (1.4–1.5 x); postmental very much wider than long; 3 pairs of enlarged chin scales, first pair usually slightly separated by 1 scale, second pair well separated by 1 scale and third pair by 3 scales.

Body scales smooth, in 22–26 longitudinal rows at midbody; paravertebral scales same size as more lateral scales, 115–138 in a single row; inner preanals overlap outer, medial pair of preanals enlarged; medial row of subcaudals same size as more lateral rows.

Snout-vent length 44–107 mm; tail bluntly rounded 0.64–0.84 x SVL; limbs totally lacking.

Colour. In both life and preservative generally light-brown to dark, greyish brown above and immaculate below; dark pigment tends to concentrate in centres of dorsal scales thereby creating a very diffuse spotted or striped effect; tip of tail black (see Cogger, 1983, fig. 137 for colour photograph of live specimen).

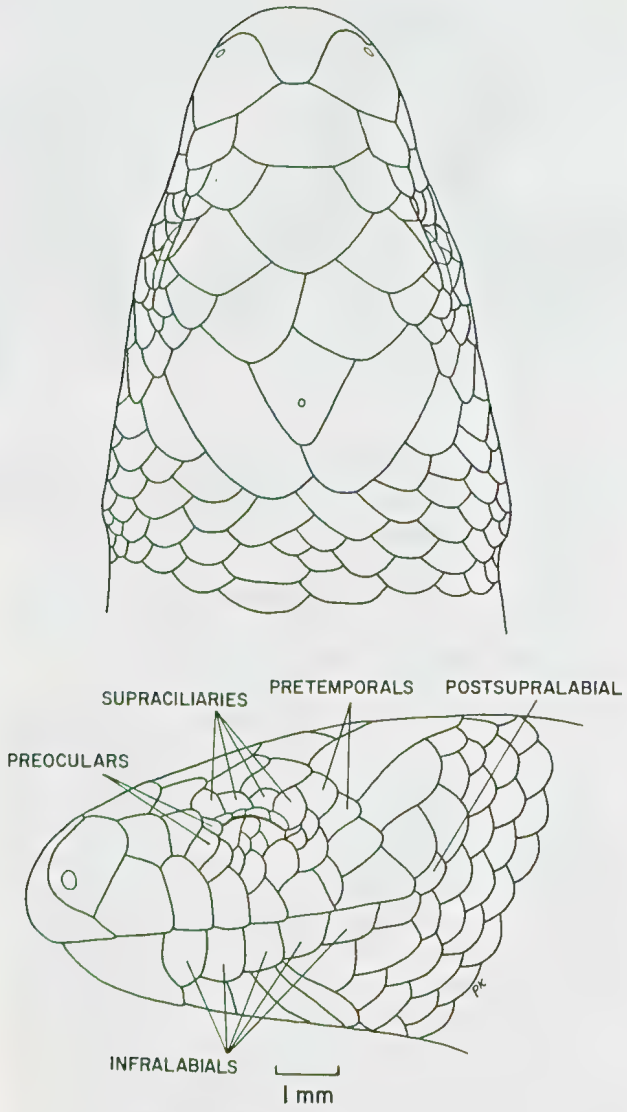

Fig. 10. Head of *Anomalopus swansoni* (AM R 11558) with certain head scales labelled.

Details of holotype. The holotype (AM R 67162) has 3 supraoculars, 26 midbody scale rows; 138 paravertebral scales; 56 presacral vertebrae, 42 postsacral vertebrae; SVL 96 mm and TL 76 mm (complete).

Distribution. Confined to an area bordered by the lower reaches of the Hunter River Valley in the north, and the northern half of the adjacent Hawkesbury River Valley in the south (Pitt Town and the Berowra area just north of the greater Sydney metropolitan area are the two southernmost known localities). Sandy Hollow, approximately 130 km from the coast in the upper Hunter River Valley, is the most inland locality (Fig. 12).

Etymology. Named for Stephen C. Swanson, photographer, natural historian and author.

Habitat and habits. Known only from fairly open forest on well-drained soils. Generally encountered under surface objects, e.g. rocks and logs, but occasionally found in rotting logs and stumps.

Reproduction. Ovoviparous. A 'no data' specimen prepared for clearing and staining (AM R 21042) contained two developing young (AM R 21043–44), and a specimen from Norah Head (AM R 112413) gave birth to two young (AM R 112414–15). The holotype (AM R 67162) contains three oviducal 'eggs' and AM R 106103 contains 3 enlarged ovarian eggs; these last two specimens measure 96 mm and 107 mm SVL and were collected on 2 Dec. and 4 Oct., respectively. Mean litter size for these four specimens is 2.5.

Anomalopus pluto Ingram
Figs 13–15

Anomalopus pluto Ingram, 1977: 52. Type-locality: McDonald Crossing, Cockatoo Ck, 115 km S of Bamaga, Cape York, Qld at 11°33'S, 142°26'E. Holotype: QM J 26261.

Material examined. In addition to the type, we have examined the following specimens. All localities are in northern Cape York Peninsula.

AM R 94360: McDonnell Ck area, 1 km E of the main N-S Peninsula Developmental Road, at 11°33′S, 142°27′E; R 94361–62, 94484–85, 112004: 15 km E of Heathlands Homestead via road to Captain Billy Beach, at 11°45′S, 142°41′E.

Diagnosis. This is the only species of *Anomalopus*, indeed the only species of Australian skink, in which the nasal extends ventrally to the upper lip (apparently through fusion with the first supralabial). It is also unique within *Vermiseps* in having the presubocular absent, the pretemporal single and the surangular fused (presumably) to the prearticular.

Description. In view of Ingram's (1977) recent description and figure of *A. pluto*, we provide only a few additional comments on the species' external morphology.

First, the most distinctive scale character of the species is the large nasal which extends ventrally to the lip. It seems virtually certain that this nasal is a complete scale resulting from the fusion of the nasal with the first supralabial. Indeed, there is a small inflection along the nasal's suture with the anterior loreal that probably represents the posterior point of the old suture between the nasal and first supralabial. If such a fusion has occurred, it means that there are really 6 supralabials instead of 5 and that the one situated directly below the centre of the eye is the fourth and not the third.

Second, there seems to be little doubt that what Ingram calls the first supraciliary is really the prefrontal. The relationship of this scale with the surrounding scales leaves little room for any other conclusion, and it is a conclusion that Ingram granted as possible.

Third, Ingram (1977, fig. 1) figures the second loreal as entering the anterior corner of the eye. In reality, there is a more-or-less vertical suture separating the second loreal from a relatively large lower preocular. It is this preocular, not the second loreal, that enters the corner of the eye (Fig. 14).

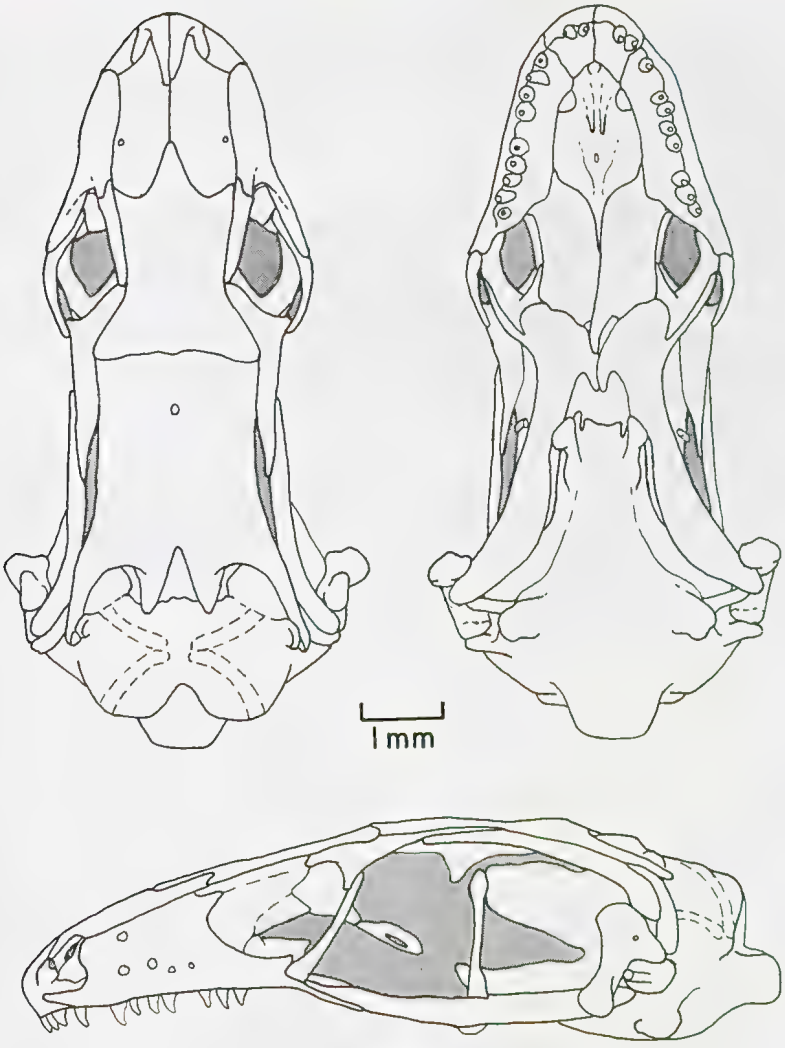

Fig. 11. Skull of *Anomalopus swansoni* (AM R 5816).

Fourth, we see only 1 large posterior supraciliary, not 2 as seen and figured by Ingram. There are thus a total of 3 free supraciliaries; the first 2 are separated from the third by the second supraocular.

For additional character states in comparison with other species of the subgenus *Vermiseps* see Table 2.

Distribution. Northern Cape York Peninsula (Fig. 12).

Habitat and habits. The holotype of *A. pluto* was "uncovered under leaf litter in a small patch of monsoon forest" (Ingram, 1977). A second specimen (AM R 94360), found near the type-locality (1 km E), was under a piece of wood on the verge of the road bordering a "vine and scrub thicket". Five other specimens (AM R 94361–62, 94484–85) were found in a very different habitat: low dense heath on white sand. These specimens were found beneath a lignotuber (N = 1) and pile of debris (N = 4) alongside a rough track. Also found in this pile of debris were *Nactus arnouxii*, *Stegonotus* sp. and *Unechis nigrostriata* (R. Sadlier, pers. comm.).

Reproduction. Nothing known.

Anomalopus gowi n. sp.

Figs 16–18

Type-material. HOLOTYPE. Queensland Museum J 42615 (formerly AM R 63128): SW side of 'Forty Mile Scrub', approximately 1.8–2.9 km NNE of Gulf Hwy via Kennedy Hwy; 18°07′S, 144°49′E; A.E. Greer; 19 June 1977.

PARATYPES. All localities are in Queensland.

AM R 32719: Minnamoolka Station, Mt Garnet; R 62465–62466, 63125–63127, 63129–30: SW side of 'Forty Mile Scrub' (approx. 1.8–2.9 km NNE of Gulf Hwy via Kennedy Hwy); R 113837: approx. 19.2 km E of Kennedy Hwy via Gulf Hwy; R 113885–89, 115248–50: approx. 7.3 km E of Woodstock PO.

BMNH AMF 35365: SW side of 'Forty Mile Scrub'; AMF 35474–79: same data as AM R 113885–89. (BMNH numbers refer to field tags.)

QM J 27617: Hervey Range, 10 km S and 35 km W of

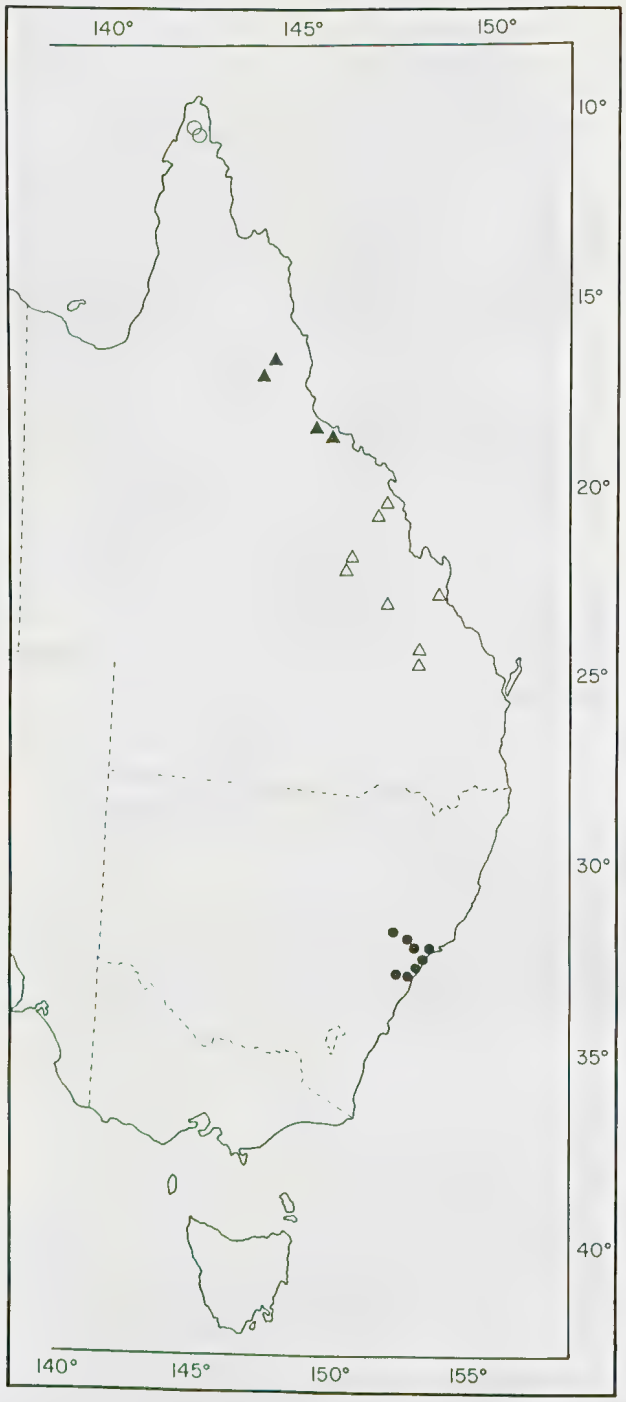

Fig. 12. Distribution of the four species in the subgenus *Vermiseps* of the genus *Anomalopus*: *A. brevicollis* (open triangles), *A. gowi* (closed triangles), *A. pluto* (open circles), and *A. swansoni* (closed circles).

Townsville; J 31050: 'Forty Mile Scrub', 40 km W of Mt Garnet.

Diagnosis. Differs from all other species of *Anomalopus* in the following combination of characters: limbs totally lacking, nasals in broad contact, and supraoculars 2.

Description. A medium-sized, limbless skink of predominantly light-tan to sandy ground colour but with the head and end of tail very dark-brown, and dark spots running through the centres of each longitudinal scale row.

Rostral trilobed with an acutely angular medial lobe projecting between nasals (which are in broad contact) to level just posterior to nostrils, and labial lobes projecting to midlength level of nasals; frontonasal much wider than long (approximately 2 x); prefrontals small, wider than long and widely separated; frontal slightly wider than long (1.2–1.3 x); supraoculars 2, first contacts frontal; frontoparietals distinct, in contact or separated; interparietal distinct, slightly larger in area than either frontoparietal and with light parietal eye spot situated centrally; parietals in short contact behind interparietal, each bordered posterolaterally by upper secondary temporal, anteriormost transversely enlarged nuchal and often a smaller scale intercalated between the two; transversely enlarged nuchals 1–4.

Nasals greatly enlarged, in medial contact for approximately one-third their entire maximum length and with nostrils situated well forward; loreal single, deeper than long; preoculars 2, lower much the larger; supraciliaries usually 3 + 1 (rarely 2 + 1), first 3 or 2 separated from last by second, or second and third, supraoculars which project laterally into supraciliary row; postoculars 2; suboculars 3, first and third largest; lower eyelid scaly; pretemporals 2, first contacted by frontoparietal; primary temporal single; upper secondary temporals 2, upper equal in size to primary and slightly larger than lower secondary; external ear opening completely covered by scaly dermis, its former position indicated by slight bulge; supralabials usually 5, rarely 6 with usually third, rarely fourth subocular; mental almost as wide or as wide as long (0.9–1.0 x); postmental much wider than long, in contact with first two infralabials; first pair of chin scales separated.

Body scales smooth, in 18–20 longitudinal rows at midbody; paravertebrals not transversely enlarged, 105–117 in a single row; inner preanals overlap outer, medial pair enlarged; subcaudals of medial and immediately adjacent rows equal in size.

Snout-vent length 49–108 mm; tail bluntly rounded, 0.75–0.94 x SVL; limbs totally lacking.

Premaxillary teeth 4–5 ($\bar{x}$ = 4.7, N = 15); presacral vertebrae 53–57; postsacral vertebrae 48–52.

Colour. The ground colour of the dorsal part of the body and most of the tail is light-tan to pale-straw; the venter of the body is light-gray. The head and end of tail are dark-brown. Between these dark extremities extend longitudinal rows of dark-brown spots, one per scale; these spots are largest on the tail and smallest on the venter. The regenerated tip of the tail has a 'dipped in ink' appearance.

In life, the iris is dark-brown and virtually indistinguishable from the pupil, and the venter has a pink suffusion due to the blood showing through the translucent scales.

Fig. 13. *Anomalopus pluto* from 15 km E of Heathlands Settlement on Captain Billy Creek Rd, Qld.

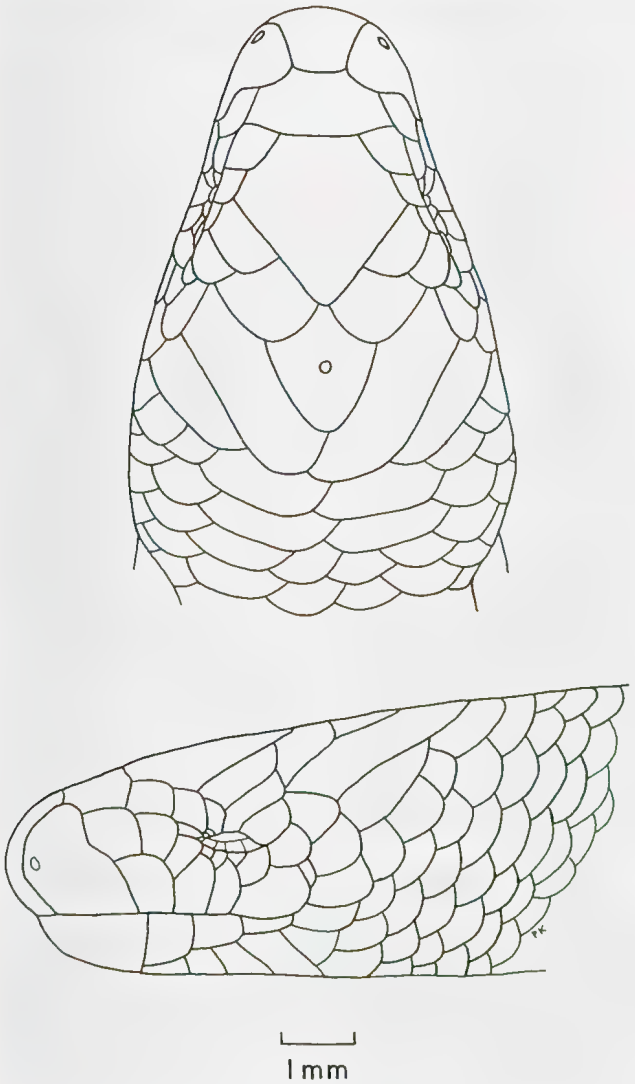

Fig. 14. Head of *Anomalopus pluto* (AM R 94362).

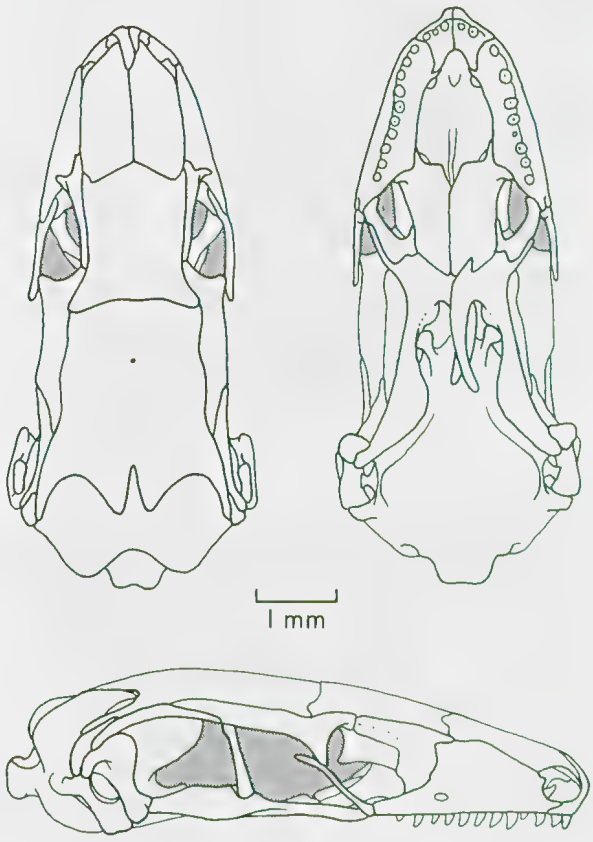

Fig. 15. Skull of *Anomalopus pluto* (AM R 94362).

Fig. 16. *Anomalopus gowi* from Forty Mile Scrub, Qld. Photo: H.G. Cogger.

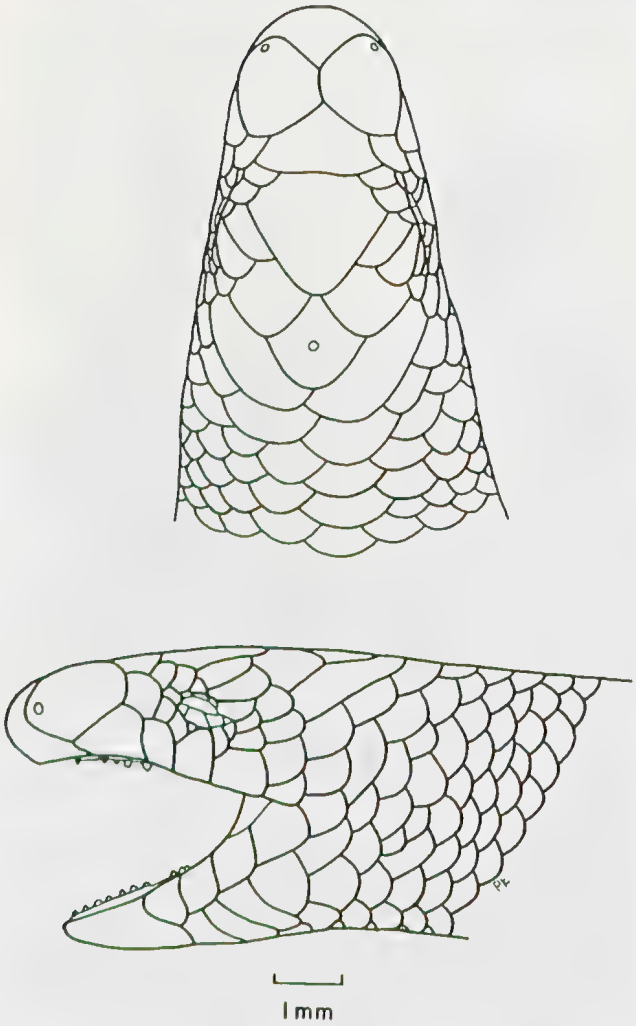

Fig. 17. Head of *Anomalopus gowi* (AM R 63128).

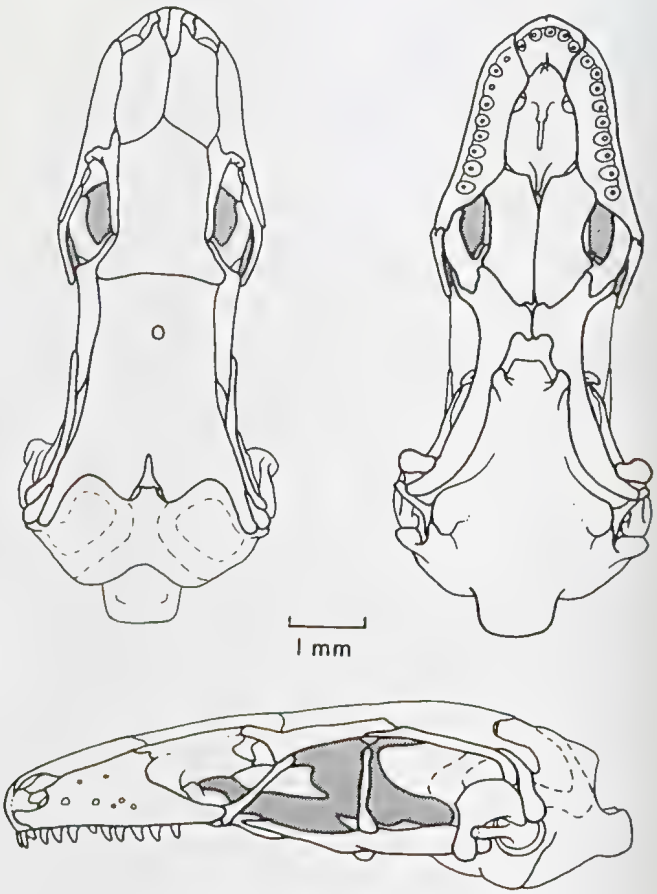

Fig. 18. Skull of *Anomalopus gowi* (AM R 63130).

Details of holotype. The holotype (QM J 42615) has a single pair of transversely enlarged nuchal scales, 4 premaxillary teeth and 57 presacral vertebrae; SVL 91 mm, TL 71 mm.

Distribution. Known only from two general areas: the vicinity between Mt Garnet and Mt Surprise and the vicinity just west and south of Townsville. Probably widespread in the drier inland area between Mt Garnet and Townsville.

Intrapopulation variation. The 15 specimens collected randomly, on the same date, at the locality just east of Woodstock, provide insight into intrapopulation variation. There are 5 males and 10 females; a sex ratio not significantly different (χ^2 = 0.86, NS) from 1:1. Females may attain larger size than males, as the largest female measures 108 mm SVL and the largest male 103 mm. Compared to males, females have more paravertebral scales (111–117, $\bar{x}$ = 113.9, SD = 2.56 vs 106–114, $\bar{x}$ = 109.6, SD = 2.97; t = 5.06***) and more presacral vertebrae (54–56, $\bar{x}$ = 54.6, SD = 0.70 vs 52–53, $\bar{x}$ = 52.8, SD = 0.45; t = 5.13***). Both trends are not uncommon in attenuate lygosomines.

Interpopulation variation. Animals from the southern end of the range appear to be larger than those from the north, and to have fewer postsacral vertebrae. The largest specimen of the ten known from 'Forty Mile Scrub' in the north measures only 90 mm SVL, whereas the largest of 15 known from Woodstock in the south measure 108 mm SVL and all but two are larger than 90 mm. The four Woodstock specimens with complete tails (1 ♂, 3 ♀ ♀) have 46–48 postsacrals whereas the six 'Forty Mile Scrub' specimens with complete tails (2 ♀ ♀, 4 indeterminate) have 49–52 postsacrals. Inability to determine sex in most of the 'Forty Mile Scrub' animals precludes a comparison of presacral vertebrae (which, because of the sexual dimorphism demonstrated above, must be made within sexes). No other differences between northern and southern populations are evident in the data.

Comparison with similar species. In lacking limbs and having the enlarged nasals in broad contact, a single loreal, 18–20 midbody scale rows, 1–4 transversely enlarged nuchals and a longitudinally spotted pattern, *Anomalopus gowi* is similar to *A. brevicollis*. It differs from this species, however, in being larger (max. SVL = 108 mm vs 83 mm) and in having 2 supraoculars instead of 3; frontoparietals usually (89 %) separate instead of always in contact; 5 supralabials instead of 6; 4 infralabials instead of 5; more paravertebrals (105–116 vs 87–104) and a lighter ground colour (see also Table 2).

Etymology. The species is named after Graeme F. Gow.

Habitat and habits. The species has been found in both sclerophyll woodland (several localities) and evergreen vine forest ('Forty Mile Scrub').

It is almost always found by turning ground cover such as rocks, logs and debris. At 'Forty Mile Scrub' it occurs primarily inside the forest under basalt rocks. At this locality it is much less common than a slightly smaller but similarly attenuate and small-limbed *Sphenomorphus* n. sp. (Greer, in press).

Reproduction. The specimens collected on 30 September 1984 from just east of Woodstock provide some insight into reproduction. Seven of the ten females in the sample of 15 are gravid. These specimens measure 99–108 mm SVL ($\bar{x}$ = 101.9 mm) and contain 1–3 ($\bar{x}$ = 2.1) enlarged ovarian (N = 1) or thinly shelled oviducal eggs (N = 6); of the non-gravid specimens, two, measuring 71 and 78 mm SVL, are clearly immature and the third, measuring 103 mm, is spent with two corporea lutea in the left ovary. There was no correlation between female SVL and clutch size (r = -0.57 NS). The shells surrounding the oviducal eggs indicate that the species is oviparous.

Anomalopus brevicollis n. sp.

Figs 19–21

Type-material. HOLOTYPE. Queensland Museum J 42616 (formerly AM R 96212): 1.0 km E of Frenchville Road via Pilbeam Drive (main road to summit of Mt Archer), Rockhampton, Qld; 23°21'S, 150°34'E; A.E. Greer; 21 August 1976.

PARATYPES. All localities are in Queensland.

AM R 13820: 32 km W of Capella; R 89277, 96200–96208, 113385–90: same locality data (different date) as holotype; R 96209–96211, 96213: same data as holotype; R 113364, 113392–95: 16.1 km N of Fitzroy R. at Rockhampton via Bruce Hwy; R 113501–04, 113790, 115245–47: 0.3 km from E end of Frenchville Rd via dirt track, Rockhampton.

ANWC 4506: Rockhampton.

BMNH AMF 35183–88: same locality data as holotype; AMF 35191–94: same data as AM R 113364 and 113392–95; AMF 35330–31, 35363, 35411: same data as AM R 113501–04, 113790 (BMNH numbers refer to field tags).

CAS 77118–77120: 32 km W of Capella.

MCZ 141079: The Diggings Rd, 6.4 km S and 1.6 km W of Eungella.

QM J 4561: Castle Ck, Dawson Valley; J 33863: 'Homevale' (21°24'S, 148°33'E); J 33870: bank of Oakey Ck, 'Homevale'; J 34056: Finch Hatton National Park in 21°24'S, 148°38'E; J 38740: Mimosa Creek, Blackdown Tableland; J 41997–41998: Cracow; J 42454: 0.5 km ENE of Old Corry Rd turnoff, via Retro.

QNPWS N 58056: Blackdown Tableland.

Diagnosis. Differs from all other species of *Anomalopus* in the following combination of characters: limbs totally lacking, nasals in broad contact, and paravertebral scales 84–102. It is also unique among *Anomalopus* in having the first sternal rib arising from the eighth presacral vertebra instead of the ninth, and unique in *Vermiseps* in having the frontal and maxilla bones in contact (thereby separating the prefrontal and nasal).

Description. A medium-sized, limbless skink of predominantly light-brown ground colour but with slightly darker head and tail and dark-brown spots running through the centers of all but the midventral scale rows.

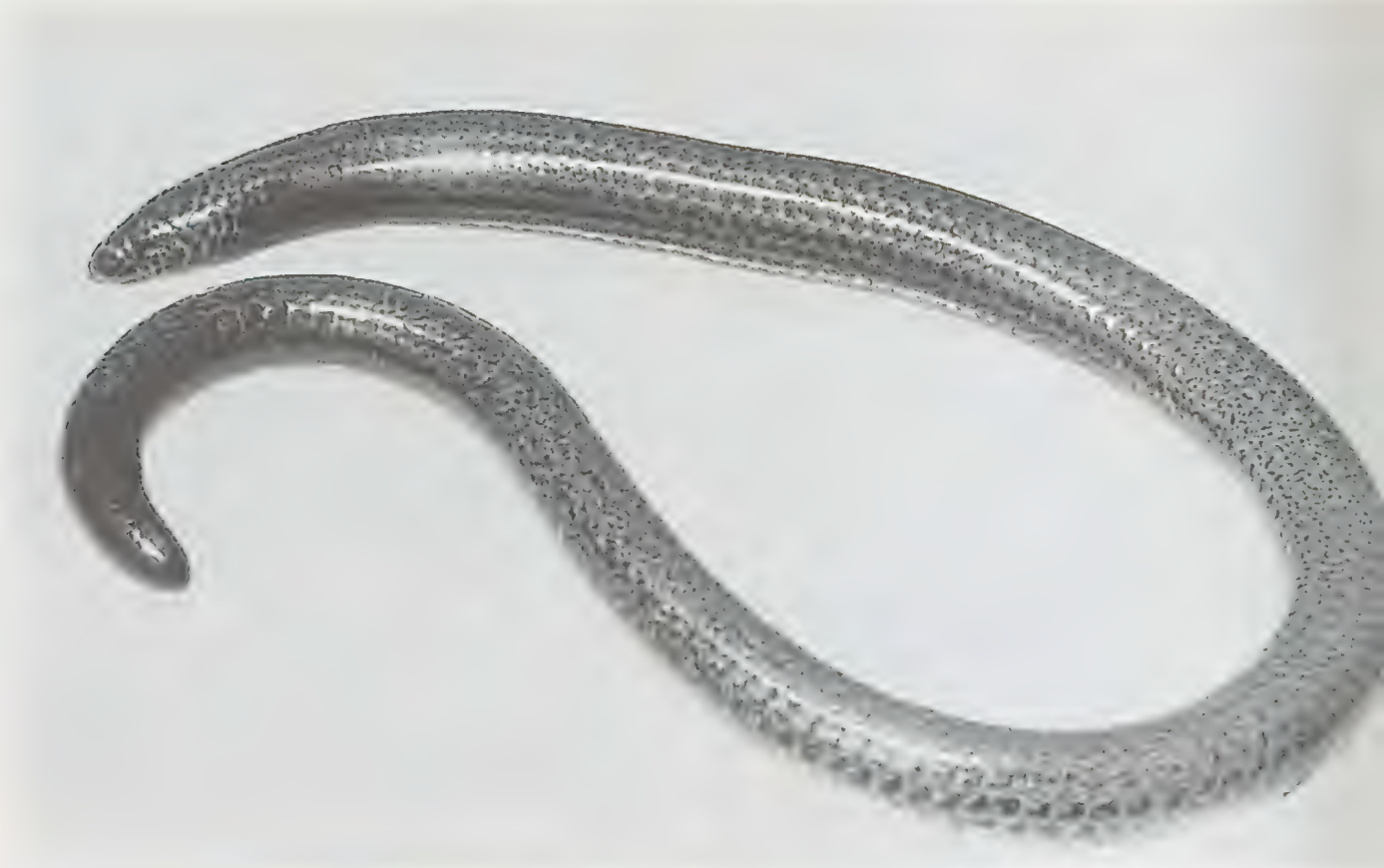

Fig. 19. *Anomalopus brevicollis* from near the base of Mt Archer, Rockhampton, Qld. Photo: A.E. Greer.

Rostral trilobed with an angular medial lobe projecting slightly between nasals (which are in broad medial contact) to approximately level with nostrils, and labial lobes projecting to midlength level of nasals; frontonasal wider than long (2.0–2.5 x); prefrontals absent; frontal wider than long (1.2–1.7 x), slightly shorter than midline length of frontoparietals and interparietals; supraoculars usually 3, rarely 2, only first contacts frontal; frontoparietals paired, usually in contact, rarely separated, each approximately equal in size to interparietal; interparietal distinct, with light parietal eye spot slightly posterior of centre; parietals in short contact behind interparietal; each parietal bordered posterolaterally by upper secondary temporal, anteriormost transversely enlarged nuchal and often a smaller scale intercalated between the two; transversely enlarged nuchals 1–4.

Nasals greatly enlarged, in broad medial contact, with nostril situated well anteriorly; loreal single, deeper than long; preoculars 2, lower much larger than upper; supraciliaries 3 + 1 or 2 + 1, first 3 or 2 separated from last by second and third, or third only, supraoculars which project laterally into supraciliary row; preoculars 2; lower eyelid scales extend into subocular row but suboculars proper absent; postocular single; lower eyelid scaly; pretemporals 2, first contacted by frontoparietal; primary temporal single; secondary temporals 2, upper either similar in size to lower or about twice its size; external ear opening absent, its former position indicated by a shallow vertical crease; supralabials 6, first largest, third or suture between third and fourth below centre of eye; postsupralabial single; infralabials 5, usually first two (rarely first only) in contact with postmental on each side; mental very large, wider than long (1.2–1.3 x); postmental much wider than long, in contact with first two (93%) or first only (7%); 3 pairs of enlarged chin scales, first pair separated by 1 scale row, second pair by 1 row and third pair by 3 rows.

Body scales smooth, in 18–20 longitudinal rows at midbody; paravertebral scales not transversely enlarged, 84–102 in a single row; inner preanals overlap outer, median pair enlarged; subcaudals of medial and adjacent rows equal in size.

Snout-vent length 39–83 mm; tail bluntly rounded, 0.86–1.17 x SVL; limbs totally lacking.

Premaxillary teeth 5–6 (N = 6); presacral vertebrae 46–49; postsacral vertebrae 48–52; cervical vertebrae 8 (instead of the more usual and primitive 9).

Colour. In preservative, the dorsal ground colour is dark, greyish brown on the head, fawn to medium-brown on the body, and medium brown becoming darker posteriorly on the tail (the tip is nearly uniform black). Pigment tends to be concentrated at the base of individual scales giving a uniform, slightly linear, pattern of spots to the top and sides of the body and base of the tail. This spotting extends onto the chin, throat, lateral edges of the venter and underside of the tail (where it becomes increasingly dense posteriorly) but the midventral area is generally unspotted or with only a few randomly scattered spots.

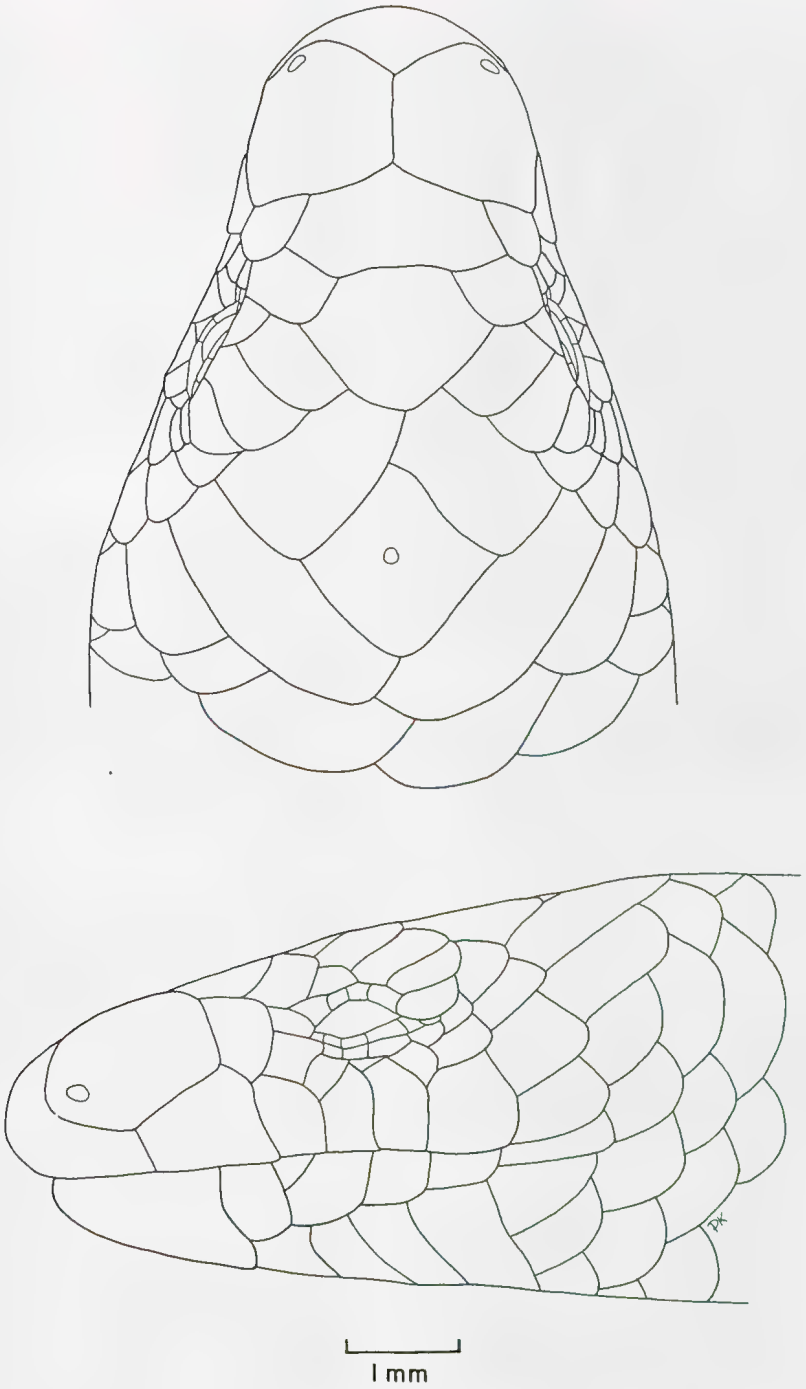

Fig. 20. Head of *Anomalopus brevicollis* (AM R 96212).

In life, the iris is as dark as the pupil and the venter light-grey or off-white with a pink suffusion due to the blood showing through the translucent scales.

Details of holotype. The holotype (QM J 42616) has 2 infralabials in contact with the postmental; 18 midbody scale rows; 3 pairs of transversely enlarged nuchals; 88 paravertebral scales; 47 pre- and 48 postsacral vertebrae; SVL 72 mm and TL 73 mm.

Distribution. Known from widely scattered localities in the area bounded roughly by Finch Hatton in the north, Clermont in the west and Theodore in the south, i.e. basically the northern half of the Mackenzie-Dawson drainage basin.

Comparison with similar species. For a comparison with the very similar *Anomalopus gowi* see this section under that species and also Table 2.

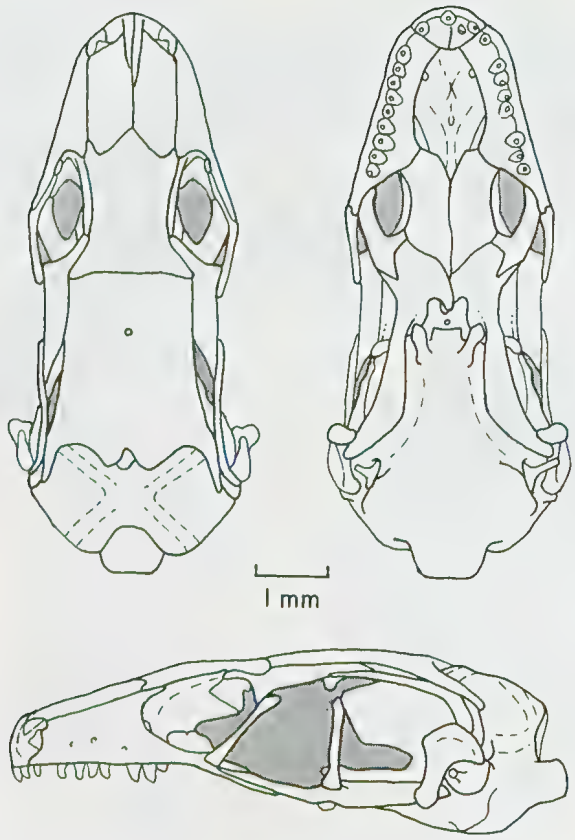

Fig. 21. Skull of *Anomalopus brevicollis* (QM J 33863).

Etymology. The name *brevicollis* derives from the Latin for 'short neck' and calls attention to reduced number of cervical vertebrae (8 instead of 9).

Habitat. *Anomalopus brevicollis* has been found in a variety of habitats ranging from dry sclerophyll forest through monsoon rainforest to permanently moist rainforest.

The specimen collected by Mr Graeme Gow near Mt Garnet (AM R 32719) was 'in open sclerophyll forest', and on the basis of general vegetation distribution, it seems likely that the specimens from both Castle Creek (QM J 4561) and 32 km W of Capella (AM R 13820) were from some kind of dry forest or woodland habitat.

The species has been collected at two sites in the Australian Museum and Queensland Museum's joint faunal survey of eastern Australian rainforests. At the Homevale site (number 10) it was found in seasonally dry, semi-evergreen vine thicket and at the Finch Hatton site (number 9) it was in moist, complex notophyll vine forest (Anonymous, 1976; Broadbent & Clark, 1976).

The three localities around Rockhampton are associated with closed forests of various kinds. One is in fairly tall, dense forest in a rocky south-facing gully at the base of Mt Archer; another is in a short, dense forest (vine thicket) on a limestone hill (this type of habitat is very common in The Caves area, north of Rockhampton), and the third (the type-locality) is in a depauperate forest on an eroded limestone reef in a northwest-facing gully on the lower slopes of Mt Archer. In all cases the closed forests stood out starkly against the surrounding dry sclerophyl woodlands. In all three habitats the animals were generally found in association with pockets of friable soil.

Habits. The critical thermal maximum temperature of five specimens ranged from 35.2–37.0°C ($\bar{x}$ = 35.8, SD = 0.65) (Greer, 1980 as *Anomalopus* sp.1)

Reproduction. The only known gravid specimens are five from the Rockhampton area (AM R 96203–04, 96210, 113389, 114084) collected in the period 21 Aug.–27 Sept. in various years. They measure 72–81 mm SVL ($\bar{x}$ = 76.4) and contain 1–2 ($\bar{x}$ = 1.8) ovarian eggs.

Morphological Trends within the Subgenus *Vermiseps*.

Three components of trunk segmentation have been assessed for the four species of *Vermiseps*: paravertebral scales, presacral vertebrae and complete inscriptional chevrons. These, plus relative tail length, increase in the series: *A. brevicollis* → *A. gowi* → *A. swansoni* → *A. pluto*. In contrast to *Anomalopus*, the trend in trunk segmentation does not follow size, as snout-vent length increases in the series *A. pluto* → *A. brevicollis* → *A. swansoni* → *A. gowi*.

Species Relationships within the Subgenus *Vermiseps*.

The phylogenetic relationships of the four species of *Vermiseps* have been inferred from a cladistic analysis of 15 characters (Table 3), the polarity of the character states having been determined with reference to the more generally primitive subgenus *Anomalopus*. The results of this analysis are presented in Figure 22.

Genus *Ophioscincus* Peters

Ophioscincus Peters, 1873: 746. Type-species: *Ophioscincus australis* Peters, 1873 (= *Lygosoma ophioscincus* Boulenger, 1887), by monotypy.

Coloscincus Peters, 1876: 532. Type-species: *Coloscincus truncatus* Peters, 1876, by monotypy.

Diagnosis. *Ophioscincus* differs from all other members of the *Sphenomorphus* group in Australia in the following combination of derived character states: nasals slightly enlarged; prefrontals separate; supraoculars 3, only first in contact with frontal; first supraciliary contacts frontal; supralabials 5, third subocular; external ear opening absent, its former position indicated by oblique crease; postsupralabial single; infralabials 5; tail ⩽ 0.95 x SVL.

Pre- and postfrontal bones in contact above orbit; postorbital absent; orbitosphenoid well ossified; quadratal conch reduced to small flange; palatal rami of pterygoids with slight to deep recurved processes;

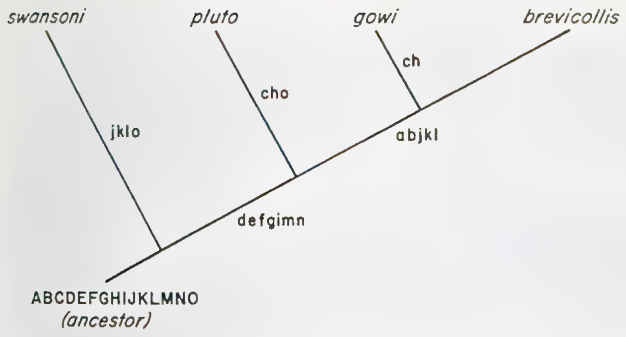

Fig. 22. Cladogram of inferred relationships of the four species of the subgenus *Vermiseps* of the genus *Anomalopus* based on an analysis of 15 characters (represented by letters A–O).

crowns of teeth squared off with distinct apical groove and rotated slightly posteromedially.

Presacral vertebrae ⩾ 43; postsacral vertebrae ⩽ 42; sternum with two attached ribs (from 9th and 10th vertebrae); mesosternum with one rib; complete inscriptional chevrons ⩾ 11; front limb lacks all elements distal to single proximal carpal; rear limb lacks all elements distal to single proximal tarsal; ischia form acute angle at symphysis with shafts paralleling those of pubes.

Parietal peritoneum lacks pigment.

Although the list of derived character states for this genus is long, the only distinctly non-burrowing feature is the peculiar shape of the tooth crowns.

Species (3). *Ophioscincus cooloolensis* n. sp.; *O. ophioscincus* (Boulenger, 1887); *O. truncatus* (Peters, 1876).

Distribution. Coastal and near coastal areas of southeastern Queensland and northeastern New South Wales (Fig. 26).

Habitat and Habits. Closed forest (all species) and wallum (*O. cooloolensis* and *O. truncatus*). Cryptozoic; generally found under surface cover.

Reproduction. Oviparous (two species).

Relationships. All but one of the derived character states of *Ophioscincus* can be interpreted as a burrowing modification and the one exception — the peculiar shape and orientation of the tooth crowns — occurs in no other member of the *Sphenomorphus* group. On the basis of this observation, all that can be said is that the possible relationships are very broad indeed and range from a relatively primitive member of the *Sphenomorphus* group (discounting burrowing related features) to a highly modified burrower (accepting these features at face value).

With regard to the latter possibility, it is significant that the genus *Isopachys* (three species) from southeast Asia shows all the derived character states of *Ophioscincus*, or their obvious further modification, except for the tooth morphology. Hence, the diagnosis above for *Ophioscincus*, less the tooth morphology, could serve equally well to diagnose an *Ophioscincus–Isopachys* group, the generic name for which would be *Ophioscincus*. This is precisely the suggestion made by Smith (1935) when the only Australian species known was *O. australis* (= *ophioscincus*), but this idea was never widely accepted (Heyer, 1972; Greer, 1977; Cogger, 1983, but see Mittleman, 1952).

Does this proposal have validity? This depends, of course, on the significance of characters that may be convergent within burrowers. In this case the list of shared 'burrowing features' is particularly long, and hence the possibility of close relationship should be considered seriously. On the other hand, given enough trials with burrowing, and there have been many in skinks, a few are likely to show remarkable similarity. The dilemma remains unresolved. The 'solution' offered here is to keep the two genera distinct. This is the conservative taxonomic position, which seems appropriate in the face of uncertainty, and it is the one that accords well with our strong suspicions about the degree of convergence amongst burrowing skinks.

Key to Species of *Ophioscincus*

1. Limbs present.....*O. truncatus*

——Limbs absent.....2

2. Prefrontals present; loreals 2; midbody scale rows 20–24.....*O. ophioscincus*

——Prefrontals absent; loreal single; midbody scale rows 18–19.....*O. cooloolensis*

Ophioscincus truncatus (Peters)

Figs 23–25

Coloscincus truncatus Peters, 1876: 532, fig. 1. Type-locality: Peale I., Moreton Bay, Qld. Holotype: ZMB 8932.

Lygosoma truncatus monswilsonensis Copland, 1952: 128, figs 2–3, pl. 6. Type-locality: Wilson's Peak, Qld. Holotype: AM R 18587.

Material examined. AM (all specimens from N.S.W. unless designated otherwise): R 6376, 115677: locality unknown; R 866 a–f: Richmond River; R 11861 a–b: Huon Brook; R 15026: Wai Wai State Forest, Macksville; R 18587: Wilson's Peak, Qld; R 19022–4: Victoria Park via Ballina; R 35187: Five Day Ck near Comara; R 44774–96, 89270: Red Scrub Flora Reserve, Whian Whian State Forest; R 44797: Brindle Ck, Wiangaree State Forest; R 44798–805: 18 km NE Wiangaree via Wiangaree State Forest Rd; R 60767: Dorrigo; R 61169–71, 71434: Brinerville area; R 96445: Mt Warning; 5 unregistered specimens: 5.1 km SE of Maleny, Qld.

MV D 1285: Qld.

QM (all specimens from Qld unless designated otherwise): J 2281: P.J. War Signal Station, Moreton I.; J 5202–4: National Park (= Lamington National Park); J 6898: Maleny; J 14143, 14148–9: no locality data; J 16872: on track to Blue Lagoon, Moreton I.; J 16873–4: near The Hut, Ocean Beach, Moreton I.; J 21942: Mary Cairncross Park via Maleny; J 21983: Point Lookout, Stradbroke I.; J 22275: Moreton I.;

Fig. 23. *Ophioscincus truncatus* from approximately 5.1 km SSE of Maleny, Qld.

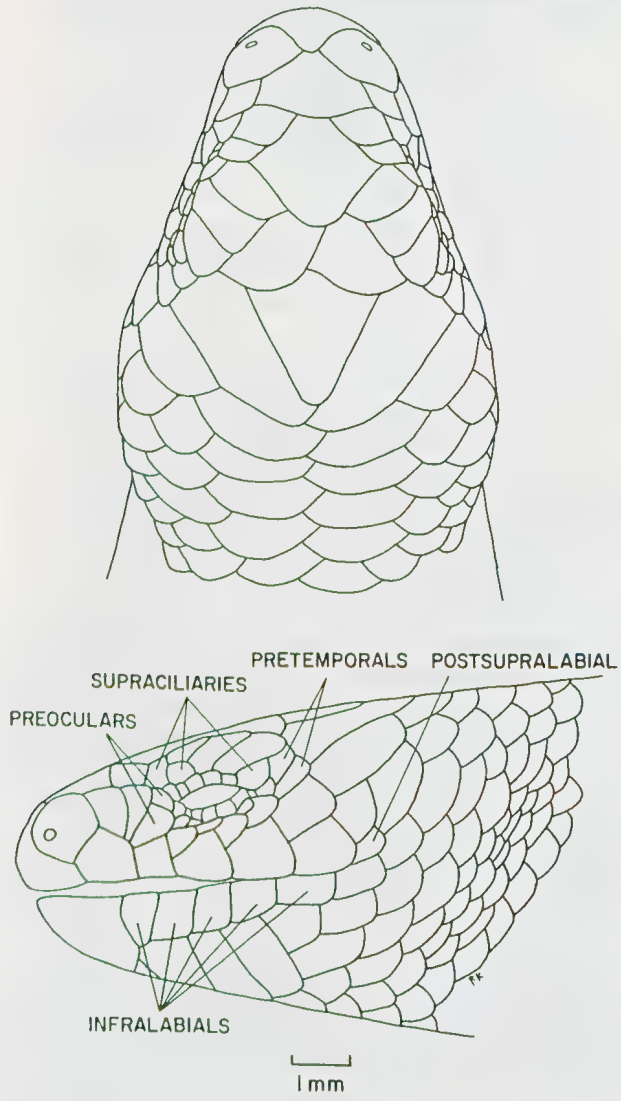

Fig. 24. Head of *Ophioscincus truncatus* (QM J 5203) with certain head scales labelled.

J 22688, 25092: Wilson's Peak; J 23642: Coolum; J 23657: Binna Burra; J 24097: Brown Lake, North Stradbroke I.; J 24860: 40 km SSE of Woodenbong, N.S.W.; J 24912: Mt Warning, N.S.W.; J 26035: Christmas Ck; J 26467: near The Head, via Killarney; J 27474: North Stradbroke I.

Diagnosis. Differs from all other *Ophioscincus* in each of the following character states: limbs visible externally, sacral diapophyses fused and ischia joined medially.

Description. Peters (1876) gave a good description and figure of *O. truncatus* in his original description and even compared it with what we recognize here as one of the species' congeners, *O. australis* (= *ophioscincus*). Copland (1952) gave his usual detailed account of the species, accompanied by a figure and photograph, when he sought to distinguish the Mt Wilson population (*O. monswilsonensis*) from the Moreton Bay populations. In light of these previous accounts and accompanying figures, we forgo a redescription of the species. For a tabular comparison between this and the other two species in the genus see Table 4.

Distribution. *Ophioscincus truncatus* is known to range from the area around Maleny in southeastern Queensland, south to Way Way State Forest just south of Macksville in northeastern New South Wales. The most inland locality is Mt Wilson on the Queensland-New South Wales border, approximately 100 km from the coast. The species is also known from Peel, Moreton and North Stradbroke Islands in Moreton Bay (Fig. 26).

Habitat. *Ophioscincus truncatus* occurs in two remarkably different habitats: rainforest and wallum (Covacevich & Ingram, 1977). Most of the mainland records are associated with rainforest while the Moreton Bay island and a few of the coastal records, e.g. Coolum, are from wallum — a dry heath and sclerophyll formation especially well developed on sandy soils. The species is notably rare or absent in 'intermediate' dry

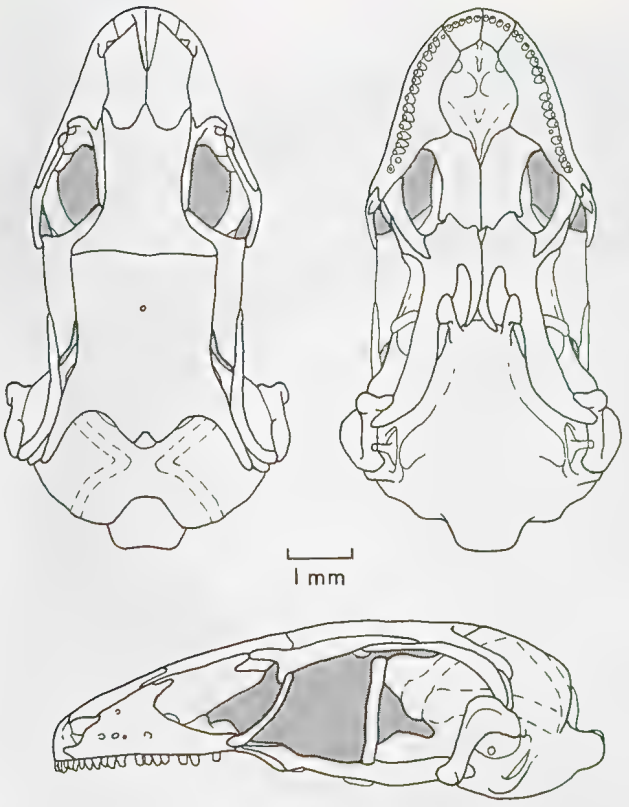

Fig. 25. Skull of *Ophioscincus truncatus* (AM R 866).

sclerophyll habitats on the mainland; it is here that *O. ophioscincus* appears to be widespread.

Reproduction. The species is probably oviparous to judge from the shelled oviducal eggs in the only two gravid females discovered (QM J 5202–5203). These two females measured 79 and 77 mm SVL and contained three and two eggs respectively. Both specimens were from Lamington National Park, Qld; no date of collection is available.

Intrapopulation variation. Twenty-one of the 25 specimens collected at random from one locality in Whian Whian State Forest, New South Wales on 21 April 1976 are large enough to be sexed reliably. They show that females (N = 15) compared to males (N = 6) have more paravertebral scales (85–95, $\bar{x}$ = 88.8, SD = 3.54 vs 79–86, $\bar{x}$ = 82.9, SD = 2.47; t = 3.71**) and more presacral vertebrae (47–50, $\bar{x}$ = 48.0, SD = 1.10 vs 45–47, $\bar{x}$ = 46.5, SD = 0.64; t = 3.26**).

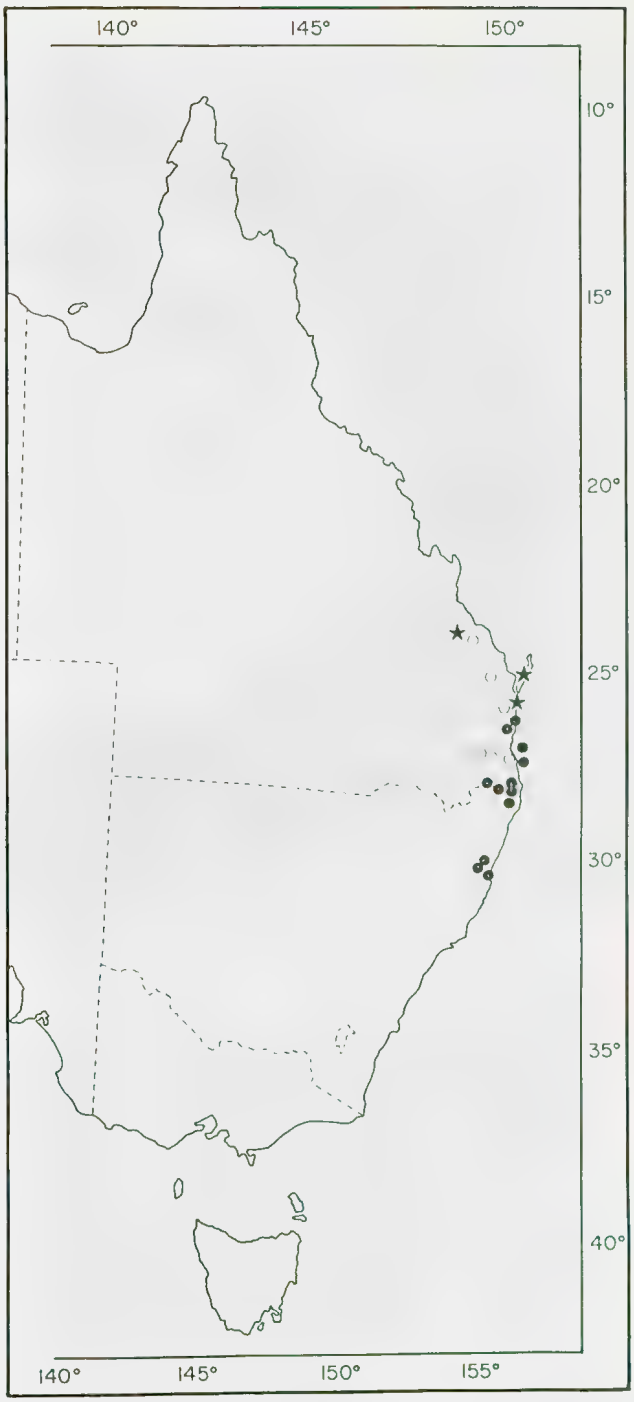

Fig. 26. Distribution of the three species of *Ophioscincus*: *O. cooloolensis* (closed stars), *O. ophioscincus* (open circles) and *O. truncatus* (closed circles).

Ophioscincus cooloolensis n. sp.

Figs 27–29

Type-material. HOLOTYPE. Queensland Museum J 31573: National Parks Headquarters on 'A' road, Fraser I., Qld; G.B. Monteith; 13 Oct. 1978.

PARATYPES. All localities are in Queensland.

AM R 64071: Tallow Wood Hill, Fraser I.; R 89276: approx 4.8 km SW Rainbow Beach PO via Gympie Rd, then 3.9 km SE via Forestry Rd.

ANWC 2541: Happy Valley, E shore of Fraser I.

QM J 27381–5: Cooloola National Park via Gympie; J 31574: same data as holotype; J 31578: Poona Lake, Cooloola; J 40092: Kroombit Creek, Kroombit Tops; J 40223: Poona Lake, Cooloola National Park; J 40224: 8 km along Freshwater Rd (from Rainbow Beach end), Cooloola State Forest; J 40225: Poona Scrub (Seary's Scrub), Cooloola; J 40226: Inskip Point (near Rainbow Beach township).

Fig. 27. *Ophioscincus cooloolensis* from Cooloola State Forest, Qld. Photo: A.E. Greer.

Diagnosis. Differs from all other *Ophioscincus* in the following two characters states, both of which are unique: prefrontals absent and presacral vertebrae ⩽ 44.

Description. Snout bluntly rounded; rostral trilobed with broad, rounded medial lobe projecting between nasals to contact frontonasal broadly, and 2 relatively narrow labial lobes, each projecting posteriorly below nasal; frontonasal wider than long (1.6–1.9 x), wider than frontal; prefrontal absent; frontal wider than long (1.2–1.4 x) and considerably shorter than midline length of frontoparietals and interparietal; supraoculars 3 or 2, only first in contact with frontal; frontoparietals distinct, in contact; interparietal distinct, larger than each frontoparietal; parietal eye spot located just posterior of centre in frontoparietal; parietals meet behind interparietal, each bordered posterolaterally by first transversely enlarged nuchal and upper secondary temporal; transversely enlarged nuchals 2–5.

Nasals moderately large, separated medially, with nostril well forward and slightly ventral of centre; loreal one; preoculars 2, lower much larger and in contact with first supralabial; subocular row narrowed or interrupted below centre of eye, presuboculars 1–2, postsuboculars 2; postoculars 2, lower much the larger; supraciliaries 3, anterior 2 separated from posterior one by second and third supraoculars; lower eyelid moveable, scaly; pretemporals 2, lower larger; primary temporal single; secondary temporals 2, upper much larger than lower, and lower only slightly smaller than primary; external ear opening absent, its former position indicated by a slightly forward-dipping vertical crease; supralabials 5, third situated below centre of eye and bordering scales of lower eyelid; postsupralabial single; infralabials 4; mental wider than long (1.6–1.7 x); postmental much wider than long (2.3–2.7 x) usually in contact with first two infralabials (92%), occasionally only first (8%); 3 pairs of enlarged chin scales, first pair in medial contact or just separated, second pair separated by single scale row and third pair by 3 rows.

Scales smooth, in 18–19 longitudinal rows at midbody; paravertebral scales 77–83, only slightly larger than those in more lateral rows; inner preanals overlap outer, medial pair appreciably larger than surrounding scales; median row of subcaudals slightly larger than more lateral rows.

Snout-vent length 54–69 mm; limbs absent, tail 0.77–0.93 x SVL, tip rounded.

Colour. In preservative, dorsum light-tan to light-brown with scattered dark-brown mottling on head and dark-brown spots (one per scale) running longitudinally

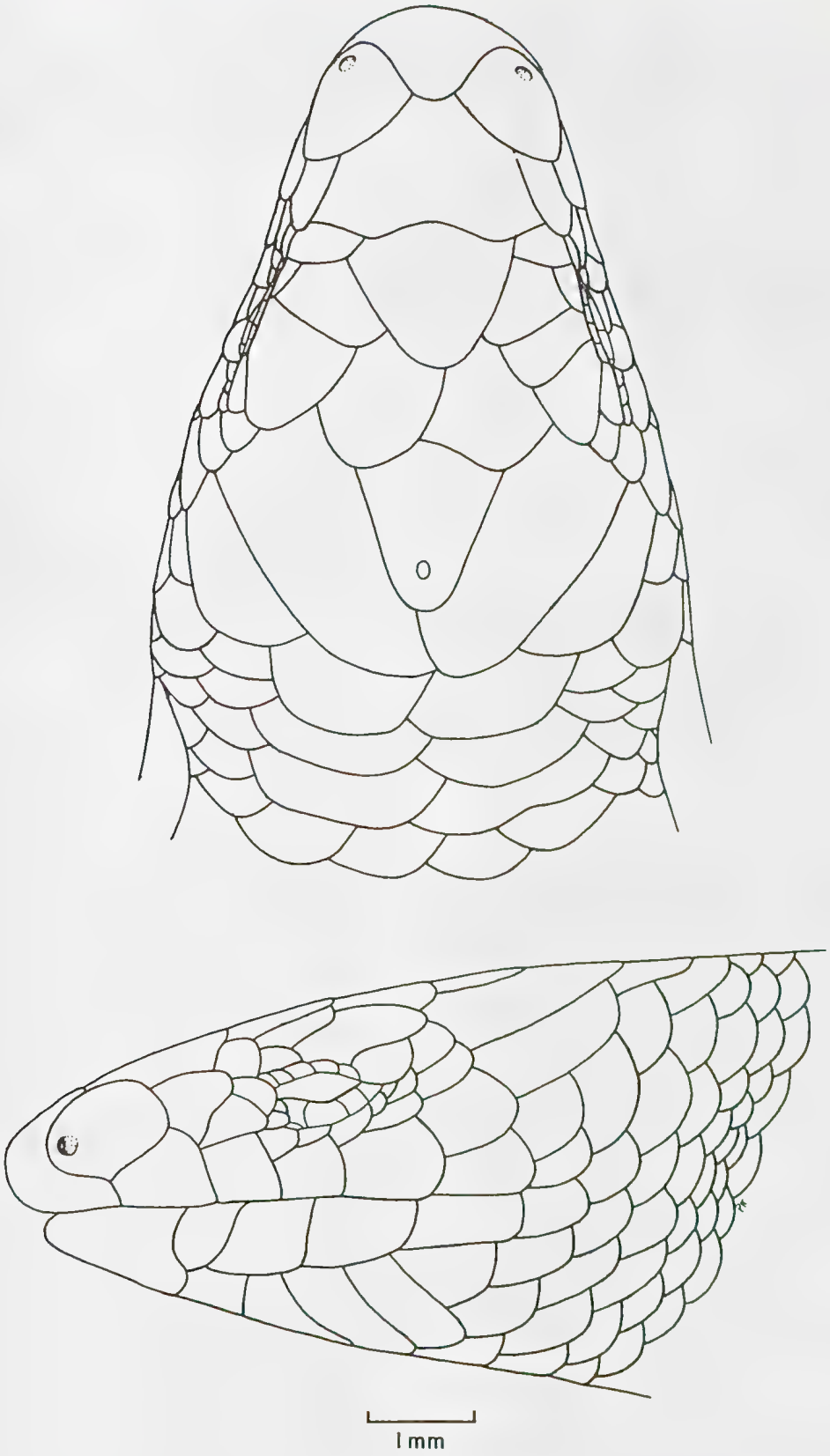

Fig. 28. Head of *Ophioscincus cooloolensis* (QM J 31573).

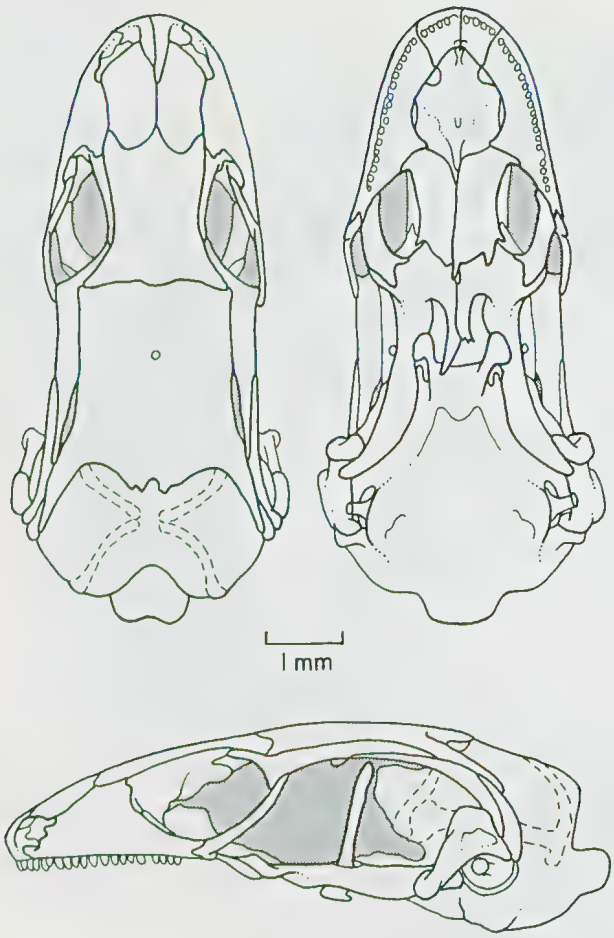

Fig. 29. Skull of *Ophioscincus cooloolensis* (QM J 27384).

on body and tail; sides with well defined, dark-brown stripe which forms a dense mottling on head and neck but a solid band over body and tail; ventral light-tan to off-white except for some dark mottling on chin and throat (which is continuous with mottling of anterior part of lateral stripe), and some solid dark colour on posterior part of tail (which is continuous with colour of posterior part of lateral stripe).

In life, one specimen (AM R 89276) was noted to have had the venter of the body (from about the pectoral area back) and tail papaya orange in colour (Greer, pers. obs.).

Details of holotype. The holotype (QM J 31573) has 2 supraoculars on the left side and 3 on the right, 2 infralabials in contact with the postmental on each side, first pair of chin scales in medial contact, 3 pairs of transversely enlarged nuchals, 18 midbody scale rows, 80 paravertebral scales, 43 presacral vertebrae, SVL 62 mm and tail regenerated.

Etymology. Named after the Cooloola area of Queensland where the species is best known.

Distribution. Known only from the coastal localities of Fraser Island and the adjacent mainland just to the south (Cooloola), and from the inland locality of Kroombit Tops in southeastern Queensland (Fig. 26).

Habitats and habits. Generally found under cover in rainforest growing on white coastal sands; also in wallum (G. Czechura, pers. comm.). 'Swims' into the substrate when uncovered.

Reproduction. A single gravid female (QM J 40092) collected on 20 January contains three enlarged ovarian eggs.

Comment. Some specimens of *Ophioscincus truncatus* have the posterior loreal truncated ventrally by the anterior loreal and lower preocular. This may be an indication of the reduction process that led to the single loreal in *O. cooloolensis*.

Ophioscincus ophioscincus Boulenger
Figs 30–32

Ophioscincus australis Peters, 1873: 747, fig. on page 746. Type-locality: Port Bowen (= Port Clinton), Queensland. Holotype: ZMB 8046.

Lygosoma ophioscincus Boulenger, 1887: 343. Replacement name for *Ophioscincus australis* Peters, preoccupied in *Lygosoma*.

Material examined. All localities are in Queensland.

AM R 47522, 47524, 47642–3, 47675, 47678, 57781, 60408, 96214–23: Bulburin State Forest.

QM J 1542–3, 2831–2: Enoggera; J 1544: Nansen, Pie Ck, Gympie; J 5067: Woody Pt, Moreton Bay; J 6260: Bald Hills, Brisbane; J 7338: Chelmer, Brisbane; J 11476: Corinda, Brisbane; J 11585–6: Gailes; J 13514: Petrie; J 13532: Samford; J 18603: Oxley Ck, Acacia Ridge; J 20289: The Gap, Brisbane; J 22291–3, 27308, 33626–30, 33681–2, 33728 (3 specimens): Bulburin State Forest; J 22328: Gympie; J 22394: 17 Mile Rocks Rd, Jindalee; J 22510, 24406: Mt Glorious; J 23171: Brackenridge, Brisbane; J 23686: Winsor Opportunity School; J 24367: Langley Rd, Camira, via Gailes; J 24370: Nudgee; J 38744, 38752: Mt Goonaneman, via Childers; J 39214–8: Forestry Deer Reserve, Kilcoy State Forest near Somerset.

MCG 27914: Port Bowen.

Diagnosis. Differs from all other *Ophioscincus* in the following character states, each of which is unique within the genus: supraciliary scale row complete; paravertebral scales ⩾ 90; premaxillary teeth 7–8; jugal short and well separated from postfrontal; parietal eye and foramen absent; supratemporal fenestra completely obliterated by close apposition of supratemporal arch (postfrontal and squamosal) to parietal; orbitosphenoid strongly ossified; maxilla enters infraorbital vacuity only narrowly, due to apposition of palatine and ectopterygoid; medial ends of clavicle narrow, and pelvic girdle reduced to widely separated puboischial rods. Only the first of these character states is primitive within the genus.

Description. Although Peter's (1873) original description of the species was accurate and accompanied by a good illustration, an expanded description will allow a more complete comparison with the species' close relatives.

Fig. 30. *Ophioscincus ophioscincus* from Bulburin State Forest, Qld. Photo: A.E. Greer.

Snout bluntly rounded; rostral trilobed with broad, rounded rostral lobe projecting between nasals to contact frontonasal broadly, and 2 relatively narrow, angular labial lobes each projecting posteriorly below nasal; frontonasal wider than long (1.5–2.0 x), narrower than frontal; prefrontals well developed but widely separated; frontal wider than long (1.4–1.8 x) and slightly shorter than midline length of frontoparietals and interparietal; supraoculars 3 or 2, only first in contact with frontal; frontoparietals paired, in contact; interparietal distinct, slightly larger than each frontoparietal; parietal eye absent; parietals meet behind interparietal, each bordered posterolaterally by transversely enlarged nuchal and upper secondary temporal; transversely enlarged nuchals 0–4.

Nasals moderately large and separated, nostril situated well forward and slightly ventral of centre; loreals 2, first deeper than second; preoculars 2, lower larger; subocular row narrowed or interrupted below eye, presubocular 1, postsuboculars 2; supraciliaries 4, in continuous series, third and fourth projecting medially to varying degrees; lower eyelid moveable, scaly; pretemporals 2; primary temporal single; secondary temporals 2, upper much larger than and overlapping lower, which is about equal in size to primary; external ear opening absent, its former position indicated by vertical crease; supralabials 5, third situated below centre of eye and bordering scales of lower eyelid; postsupralabial single; infralabials 4; mental wider than long (1.7–2.1 x); postmental much wider than long (2.1–3.1 x), usually in contact with first infralabial only (98%), rarely with first two (2%); 3 pairs of enlarged chin scales, first and second pairs separated by single scale row, third pair by 3 scale rows.

Body scales smooth, in 20–24 longitudinal rows at midbody; paravertebral scales 94–113, only slightly wider than those in more lateral rows; inner preanals overlap outer, medial pair appreciably larger than surrounding scales; median row of subcaudals slightly larger than more lateral rows.

Snout-vent length 39–97 mm; limbs absent; tail 0.59–0.88 x SVL, tip bluntly rounded.

Colour. In preservative, dorsum is light to medium tan with scattered darker brown mottling on head and dark brown spots (one per scale) forming longitudinal lines on body and tail; sides with well defined, dark-brown stripe which begins as dense mottling on the head and neck but quickly coalesces to extend the length of the body and tail; venter light-tan to off-white except for dark mottling on chin and throat which is continuous with anterior part of lateral stripe, and dark-brown colour on posterior four-fifths of the tail which is continuous with solid, dark colour of posterior part of lateral stripe.

In life, small individuals (SVL = 37–46 mm, N = 4) were noted to have the light ventral areas pale-yellow, and large individuals (SVL = 57–89 mm, N = 5) orangish yellow (Greer pers. obs., on Bulburin State Forest specimens).

Distribution. *Ophioscincus ophioscincus* is known only from southeast Queensland in an area from Bulburin State Forest in the Many Peaks Range, south

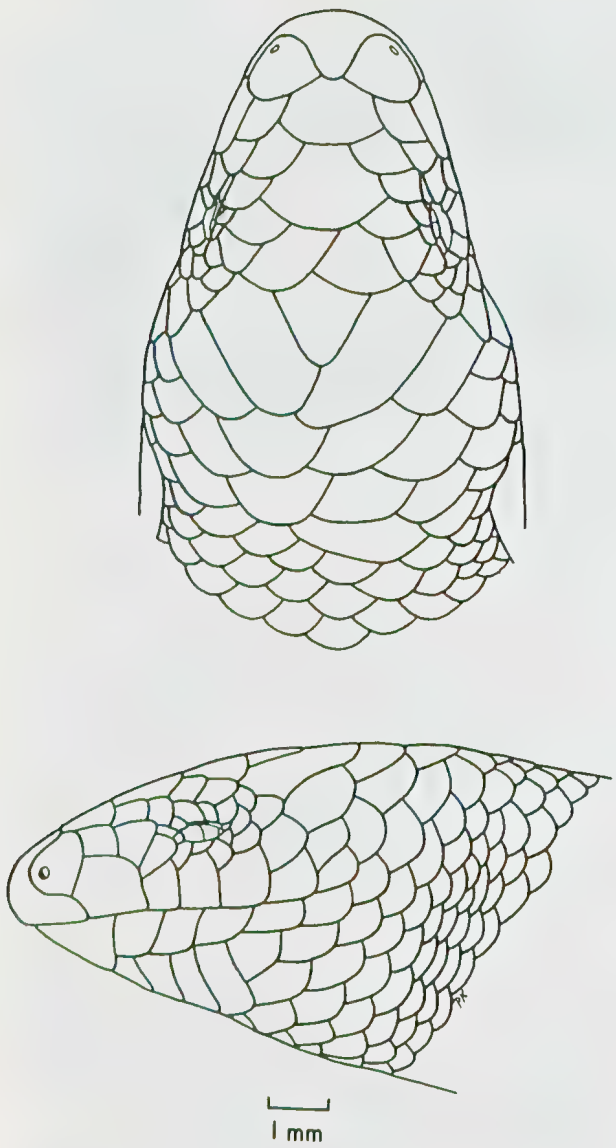

Fig. 31. Head of *Ophioscincus ophioscincus* (QM J 13514).

to the lower reaches of the Brisbane River Valley. The species has not been found on any of the offshore islands of southeast Queensland (Fig. 26).

Peters' type-locality of Port Bowen, situated approximately 100 km NNE of Rockhampton at 22°29′S, 150°43′30″E (Wells, 1848), is approximately 230 km NNW of the nearest modern and well established locality at Bulburin State Forest. Because of this 'disjunction' and an even more egregious one for another Peters' Port Bowen type (*Lygosoma scutirostrum*; see Greer, 1983: 42–44), the locality is taken to be in error.

The species ranges in altitude from near sea level to approximately 610 m at Bulburin State Forest.

Habitat. Rainforest, both within the forest and in clearings (pers. obs.).

Reproduction. We have found four gravid females in collections. All have shelled oviducal eggs indicating

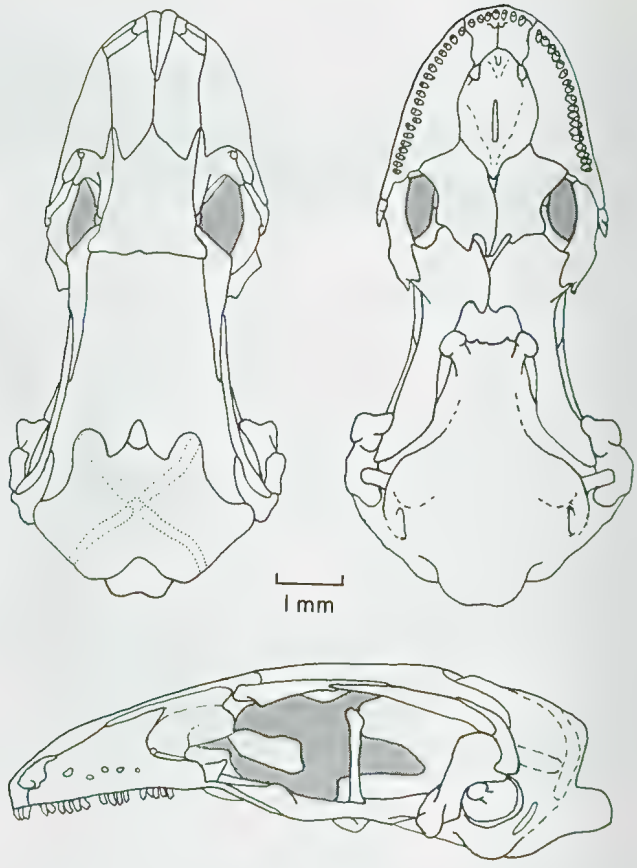

Fig. 32. Skull of *Ophioscincus ophioscincus* (AM R 47642).

the species is oviparous. One female (QM J 7338) collected from the Brisbane area measured 68 mm SVL and contained three eggs; three others (QM J 30607, 31613–14) collected from Ravensbourne on 7–8 January 1978, measured 93, 97 and 97 mm SVL and contained 2,3 and 2 eggs, respectively.

Morphological Trends within the Genus *Ophioscincus*.

Three measures of trunk segmentation have been assessed in the three species of *Ophioscincus*: paravertebral scales, presacral vertebrae, and complete inscriptional chevrons. All three, plus midbody scale rows, increase in the series *O. cooloolensis* → *O. truncatus* → *O. ophioscincus*. This series also follows an increase in snout-vent length but places the one limbed form between the two limbless (externally) forms. Thus, as in the case with *Anomalopus*, trunk segmentation seems to be more closely related functionally to size increase than to limb loss.

Species Relationships within the Genus *Ophioscincus*.

The phylogenetic relationships of the three species of *Ophioscincus* have been inferred from a cladistic analysis of eight characters (Table 5), the polarity of the character states being determined with reference to the character state in a generalized member of the

Sphenomorphus group. On the basis of this analysis *O. cooloolensis* and *O. ophioscincus* share the largest number of derived character states (characters E–H) and hence may be presumed to be each others closest living relatives. However, all the characters indicating this relationship are postcranial and if one takes the attitude that they may be simply manifestations of a single, more general feature of limb reduction, this hypothesis fails, leaving as equally weak alternative hypotheses: either an *O. truncatus–O. ophioscincus* (characters A and D) or an *O. truncatus–O. cooloolensis* (characters B and C) relationship.

Genus *Coeranoscincus* Wells & Wellington

Coeranoscincus Wells & Wellington, 1984: 87. Type-species *Ophioscincus frontalis* De Vis, 1888, by original designation.

Diagnosis. *Coeranoscincus* differs from all other members of the *Sphenomorphus* group in Australia in the following combination of derived character states: snout slightly conical; nasals slightly enlarged; prefrontals separated (although often only barely in *C. frontalis*); supraoculars 3 (primitive supraoculars 3 and 4 fused or one lost — cf. *Anomalopus* (*Vermiseps*) and *Ophioscincus*); first supraciliary contacts frontal; supraciliaries 6 or less; supralabials 6, fourth below centre of eye; infralabials 5; ear opening absent; size large (maximum size of smaller species = 195 mm).

Maxilla-frontal contact; pre- and postfrontals closely apposed above orbit; quadratal conch lacking; supratemporal fenestra obliterated by apposition of supratemporal arch to parietal; premaxillary teeth ⩽ 8; teeth pointed and recurved; palatal rami of pterygoids moderately separated.

Presacral vertebrae ⩾ 52; complete inscriptional chevrons ⩾ 12; manus lacks intermedium and pisiform, distal carpals 1 and 5 and metacarpal 1, and has phalanges reduced to 0.2.3.3.0 or less; pes has astragalus and calcaneum distinct, lacks metatarsal 1 and has phalanges reduced to 0.2.3.3.0; sternal ribs ⩽ 2; mesosternal ribs 1.

Parietal peritoneum lacks pigment.

Three characters in the foregoing suite are not necessarily associated with burrowing and therefore provide the primary reason for hypothesizing the monophyly of the group: large size, premaxillary teeth ⩽ 8, teeth pointed and recurved, and palatal rami of pterygoids slightly separated medially.

It should be noted that this diagnosis differs substantially from that of Wells & Wellington (1984).

Species (2). *O. frontalis* (De Vis, 1888) and *O. reticulatus* (Günther, 1873).

Distribution. Widely disjunct along the coast and near coastal areas of eastern Australia: northeastern Queensland, southeastern Queensland and northeastern New South Wales (Fig. 37).

Habitat and habits. Tall open forest and closed forest (rainforest); primarily the latter. Cryptozoic; generally found under surface cover or in decaying logs.

Reproduction. Oviparous (one species).

Relationships. None of the characters, as understood at this time, offer any particularly cogent insight into the relationships of *Coeranoscincus*.

Key to Species of *Coeranoscincus*

1. Limbs present.....*C. reticulatus*

——Limbs absent.....*C. frontalis*

Coeranoscincus reticulatus (Günther)

Figs 33–36

Chelomeles reticulatus Günther, 1873: 146. Type-locality: Clarence River, N.S.W. Holotype: BMNH 1946.8.3.25.

Material examined. AM R 644: Clarence R., N.S.W.; R 2201: Tweed R., N.S.W.; R 3317, R 6375: locality unknown; R 4795: Clarence R., N.S.W.; R 17804: Richmond Range, N.S.W.; R 18707, 18742: Binnaburra, Qld; R 55066: Whian Whian State Forest, N.S.W.; R 57076: Grafton, N.S.W.; R 89096, 89281: Grady's Ck Flora Reserve, Wiangaree State Forest, N.S.W.; R 98376: 0.5 km S Qld border via Mt Lion Rd, N.S.W.; R 111131: Grafton, N.S.W.

MV D 9056: Emu Vale, near Warwick, Qld.

QM J 4390: Tambourine Mt, Qld; J 6217: Beechmont, Qld; J 14507, 22692: Lamington National Park, Qld; J 22616: Binna Burra, Qld; J 24348: 6 km SE of Maleny, Qld; J 24407: Cooloola State Forest, Qld; J 24408–12: Lamington National Park, Qld; J 25409: Cunningham's Gap National Park, Qld.

WAM R 43856: south of Lamington, Qld.

Diagnosis. Differs from all other lygosomines with a digital formula of 3/3 (*Eumecia achietae* (some), *Hemiergis decresiensis*, *Lerista fragilis*, *L. haroldi*, *L. muelleri*, *L. terdigitata* and *Saiphos equalis*) in having distinct prefrontals and 2 loreals instead of 1 (*Saiphos*), in having lost the external ear opening (*Eumecia* and *Lerista*), or in having a scaly lower eyelid instead of an eyelid with a clear window (*Hemiergis*). For a comparison with the only other species in the genus, see below and Table 6.

Description. As the last comprehensive description of this species was provided nearly a century ago (Boulenger, 1887) and the species is still somewhat rare in collections today, a redescription based on currently important characters may be useful.

In general appearance, a long, attenuate skink with small front and rear tridactyl limbs and a plain brown to dark, cross-banded colour pattern.

Snout, bluntly conical; rostral trilobed with moderately deep median lobe projecting between nasals to make contact with frontonasal, and two truncated lateral lobes ending at level of nostril; frontonasal slightly wider than long; prefrontals large but separated; frontal slightly longer than wide, approximately equal to, or slightly shorter than, midline length of frontoparietals and interparietal; supraoculars 3, first 2 in contact with frontal; frontoparietals distinct, each shorter than interparietal; interparietal distinct, with distinct parietal eye spot; parietals meet behind

Fig. 33. *Coeranoscincus reticulatus* from Wiangaree State Forest, N.S.W. Photo: A.E. Greer.

Fig. 34. *Coeranoscincus reticulatus* from Richmond R., N.S.W showing the reticulated ventral pattern which gives the species its name. Photo: H.G. Cogger.

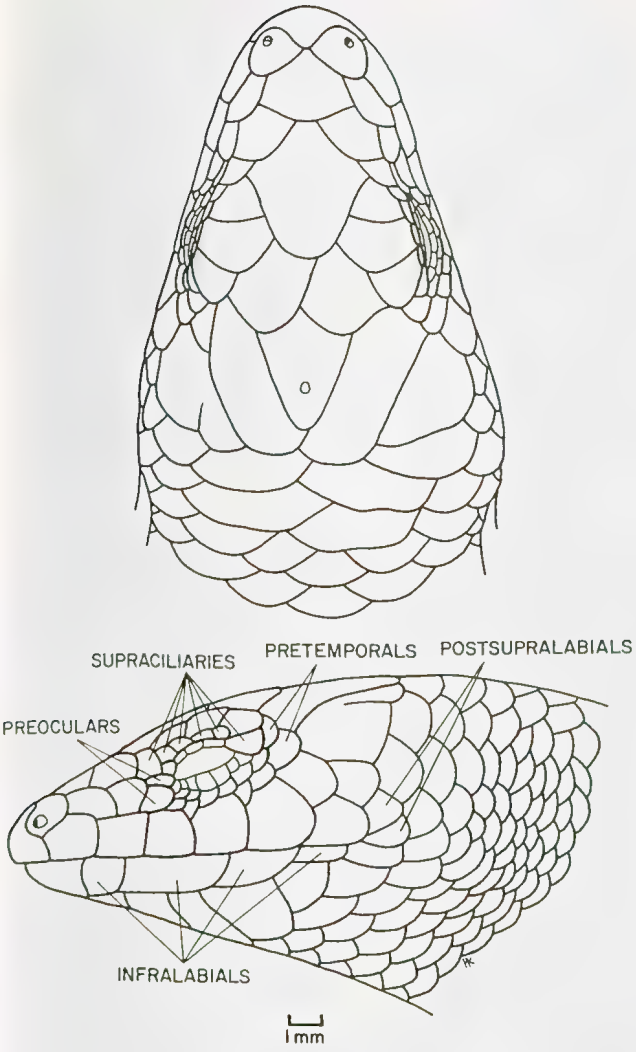

Fig. 35. Head of *Coeranoscincus reticulatus* (AM R 55066) with certain head scales labelled.

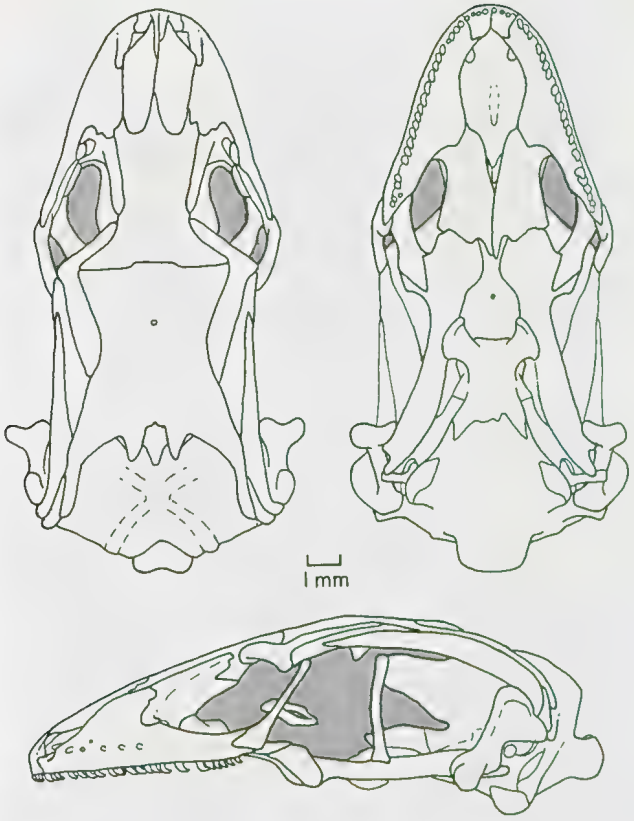

Fig. 36. Skull of *Coeranoscincus reticulatus* (AM R 4795).

interparietal, each bordered posterolaterally by upper secondary temporal and anterior nuchal, and often a third scale intercalated between the two; nuchals differentiated, 2–4 (mode = 4).

Nasals slightly enlarged, separated, with nostril situated well forward and slightly below centre; loreals 2; preoculars 2, lower much the larger; subocular scale row interrupted or narrowed appreciably below centre of eye; presuboculars usually 2, rarely 1; postsuboculars 2; supraciliaries 5–6 (mode = 6), first largest and in contact with frontal, last projects between last supraocular and first pretemporal; lower eyelid scaly; pretemporals two; primary temporal single; secondary temporals 2, upper much the larger and overlapped by lower; external ear opening absent, its former position indicated by a conical depression in a nearly vertical crease; supralabials 6, fourth subocular; postsupralabials usually 2, occasionally 1; mental moderate in size; postmental as large as mental, in contact with first 2 infralabials on either side; enlarged pairs of chin scales 3, first pair in contact, second pair separated by 1 scale row, and third by 3.

Body scales smooth, in 23–28 longitudinal rows at midbody; paravertebral scales only slightly wider than more lateral rows, 109–125 in a single row; inner preanals overlap outer, medial pair enlarged; median row of subcaudals slightly wider than immediately adjacent rows.

Snout-vent length 67–195 mm; front leg 0.04–0.07 x SVL, with 3 very short, clawed toes of which middle is largest; rear leg with 3 very short, clawed toes of which middle is largest, 0.04–0.09 x SVL; tail pointed, 0.98–1.47 x SVL.

Colour. Individuals approximately 70 mm SVL and shorter have very conspicuous dark crossbands which are large and distinct anteriorly but become broken and diffuse posteriorly. Generally, there is a rather broad dark crossband or blotch on the head extending down into the ocular area, a slightly narrower one across the nape, and numerous posterior bands which are still narrower and more variable. Adults never seem to retain the dark head band except as a dark ocular blotch, while the nape and body bands may be either retained throughout life (albeit against a generally darkening ground colour) or lost from back to front, the ultimate in this trend being the total loss of banding. The venter is usually heavily reticulated with dark colour.

In life, an adult male (AM R 89281) had the labial area and side of head and neck back to the ear suffused

with light-yellow, the chin and throat even paler yellow and the rest of the venter grey (pers. obs.; see also Czechura, 1974).

Distribution. *Coeranoscincus reticulatus* occurs in the ranges and lowlands between Cooloola in southeast Queensland and Grafton in northeastern New South Wales (Fig. 37).

Habitat. Most specimens for which there are data have been found in closed forest (Czechura, 1974; McDonald, 1977 and pers. obs.), but there is at least one record from "all open layered eucalyptus forest" (McDonald, 1977).

Diet. McDonald (1977) found stomach contents in four of the 18 specimens he examined. These comprised three earthworms, one coleoptera larva and one indeterminable insect. The earthworms are especially interesting because large earthworms are relatively common in the closed forest habitats of *Coeranoscincus* and may be the prey to which their pointed, recurved teeth are adapted.

Reproduction. McDonald (1977) examined four gravid females and I have examined one (WAM R 43856). These females ranged 100–192 mm SVL ($\bar{x}$ = 154 mm) and contained 2–6 oviducal eggs ($\bar{x}$ = 4.2). The dates of collection available for three females were in the period 20 Oct.–12 Dec. The thickness of the shells of the eggs examined by me indicated that the eggs would have been laid. McDonald (1977) also reported three females with large ovarian follicles. The SVLs for these females ranged 135–164 ($\bar{x}$ = 148 mm); no dates of collection were available, however, and no follicle counts were given.

Coeranoscincus frontalis De Vis
Figs 38–40

Ophioscincus frontalis De Vis, 1888: 823. Type-locality: Geraldton (= Innisfail), Qld. Syntypes: QM J 243, 11499, 19737–41.

Material examined. All localities are in northeast Queensland.

AMNH 27295: Ravenshoe District; 83937: Malanda Falls.

AM R 3823: Queensland; R 4006: Mt Bartle Frere; R 16627: Atherton; R 49086: Mt Speck; R 55074: Thornton Peak area; R 61297: Milla Milla; R 89278–80: vicinity of "The Boulders", West of Babinda; R 91063: Yuccabine Ck at Kirrama State Forest Rd (29.3 km W of Bruce Hwy via Kirrama State Forest Road).

ANWC 3454: Severin State Forest, Atherton; 4114: Atherton.

QM J 243, 11499: Geraldton (= Innisfail); J 5215: Aloomba; J 5336: Barrine; J 13139: Euramo; J 13139: Mt Kalorama;
J 19737–19741, 22172: locality not known.

QNPWS N 12268: Mt Speck.

Diagnosis. Differs from the only other species of *Coeranoscincus* in being totally limbless.

Description. A long limbless skink with a dark lateral band in juveniles but this diminishes with age to give a plain, brown ground colour in adults.

Snout bluntly conical; rostral trilobed with distinct median lobe projecting between nasals to contact frontonasal, and 2 slightly shorter, labial lobes extending to level of nostril; frontonasal about as long as wide; prefrontals large, narrowly to moderately separated; frontal longer than wide, approximately equal to midline length of frontoparietal and interparietal; supraoculars 2 or 3, first 1 or 2 contact frontal; frontoparietals distinct, broadly contacting to narrowly separated, each smaller than interparietal; interparietal distinct, with distinct parietal eye spot; parietals meet behind interparietal, each bordered posterolaterally by upper secondary temporal, undifferentiated body scale or transversely enlarged nuchal and often a third scale intercalated between these 2; nuchals 0–4.

Nasals slightly enlarged, well separated, with nostril in ventral corner; loreals 2; preoculars 2; supraciliaries 4 or 5, first much the largest and in contact with frontal, penultimate projecting medially between last 2 supraoculars, and last projecting medially between last supraocular and first pretemporal; subocular scale row complete, but anterior scales small, last 2 large; lower eyelid scaly; pretemporals 2; primary temporal single; secondary temporals 2, upper much the larger (long), overlapping lower which is about same size as primary; external ear opening absent, its former position indicated by a nearly vertical crease; supralabials 6, fourth subocular; postsupralabials 2; mental moderate in size; postmental about equal in size to mental, in contact with first 2 of 5 infralabials; enlarged pair of chin scales 3, members of first pair in contact, those of second pair separated by 1 scale row, and those of third by 3 rows.

Body scales smooth, in 26–34 longitudinal rows at midbody; paravertebral scales equal in size to more lateral row, 151–197 in single row; inner preanals overlap outer, medial pair enlarged; median row of subcaudals just slightly wider than more lateral rows.

Snout-vent length 70–291 mm; no external trace of limbs; tail 0.47–0.57 x SVL.

Colour. Specimens generally smaller than about 130 mm SVL have a distinct colour pattern. The dorsum of the body and tail is dark-brown, often with slightly darker longitudinal stripes as in the adults, but the top of the head, the nape and the sides of the neck are generally light-cream colour with the exception of dark pigment concentrated around the eyes and ears. A very distinct dark stripe begins on the side of the chin and extends posteriorly along the side of the throat to a point just posterior to the level of the ear where it turns slightly upward to just below the level of the ear and extends posteriorly to just past the vent before breaking up into a series of evenly spaced, dark, vertical dashes connected dorsally by a thin longitudinal stripe.

Depending on their size, adults retain elements of this pattern, but suffusion of dark pigment over the nape and head, and the loss of dark pigment from the lateral stripe results in a nearly uniformly coloured dorsum in

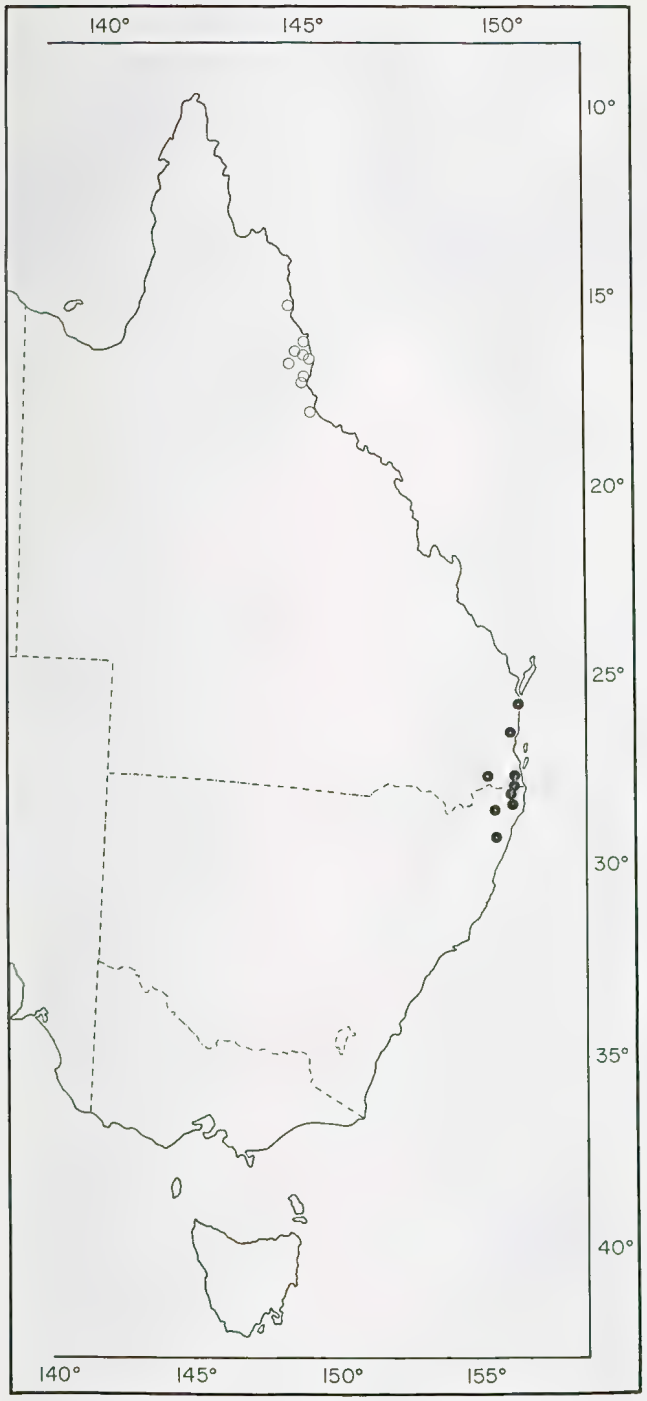

Fig. 37. Distribution of the two species of *Coeranoscincus*: *C. reticulatus* (closed circles) and *C. frontalis* (open circles).

the largest individuals. There is no polymorphism as in *C. reticulatus*.

In life, the venter of juveniles below the dark lateral stripe can vary from pale, greenish yellow to a very bright orange. In adults the venter is a pale, pinkish yellow anteriorly, becoming increasingly yellow posteriorly until maximum intensity of pale-yellow is reached over the posterior third of the body and entire underside of the tail.

Distribution. *Coeranoscincus frontalis* is known only from the coastal ranges and lowlands of northeastern Queensland, and in an area between Thornton Peak in the north and Mt Speck in the south. The most inland locality is Atherton, approximately 55 km from the coast.

Habitat. The species is known only from moist rainforest where it is generally found in rotten logs or under surface cover such as logs and rocks.

Habits. Despite the species' extremely long, sharply pointed teeth, none of the specimens we have handled (N = 4) ever attempted to bite.

Comparison of the Two Species of *Coeranoscincus*.

Meristic features of the two species are compared in Table 6 and the non-meristic below.

The **prefrontal scales** are slightly larger and closer together in *C. frontalis* than in *C. reticulatus*.

The **upper secondary temporal** overlaps the lower secondary in *C. frontalis* but the reverse is true in *C. reticulatus*.

The total **number of premaxillary teeth** is eight in *C. reticulatus* (N = 2) and seven in *C. frontalis* (N = 1).

In *C. reticulatus* the **crowns of the teeth** are flattened, pointed and 'twisted' posteriorly. The edge of the flattened points have a very narrow groove rendering the tooth bicuspid. There is also a shallow groove running along the outer curvature of the tooth. In *C. frontalis* the teeth are conical, very sharply pointed and strongly recurved, i.e., fang-like. A very narrow apical groove is evident on some of the larger teeth, rendering them biscuspid, but there is no groove running along the outer length of the teeth.

A long thin **postorbital bone** extends posteriorly to the parietal in *C. reticulatus*, but there is no distinct postorbital in *C. frontalis*.

The dorsal (postfrontal) process of the **jugal** is well developed in *C. reticulatus* but is reduced to a tapering, thin 'wisp' in *C. frontalis*.

The **palatal rami of the pterygoids** are relatively 'thin' and diverge slightly from the midline in *C. frontalis* but they are 'heavy' and medially expanded in *C. reticulatus*.

There is a short, stout midventral ridge between the **basipterygoid processes** in *C. reticulatus* but no such ridge in *C. frontalis*.

The **fenestra rotunda** is large in *C. reticulatus* but reduced to a tiny foramen in *C. frontalis*.

The **surangular** is distinct in *C. frontalis* but it is fused to the articular and prearticular in *C. reticulatus*.

The **front limb** is tridactyl with a phalangeal formula of 0.2.3.3.0 in *C. reticulatus* but is reduced to a vestige of the humerus which is not visible externally in *C. frontalis*.

In *C. reticulatus* the **pectoral girdle** differs little from the primitive scincid condition; the major difference is that only two ribs (from the ninth and tenth presacral vertebrae) contact the sternum instead of three, and one or no rib contacts the mesosternum instead of two. In

Fig. 38. *Coeranoscincus frontalis* from near 'The Boulders' just west of Babinda, Qld.

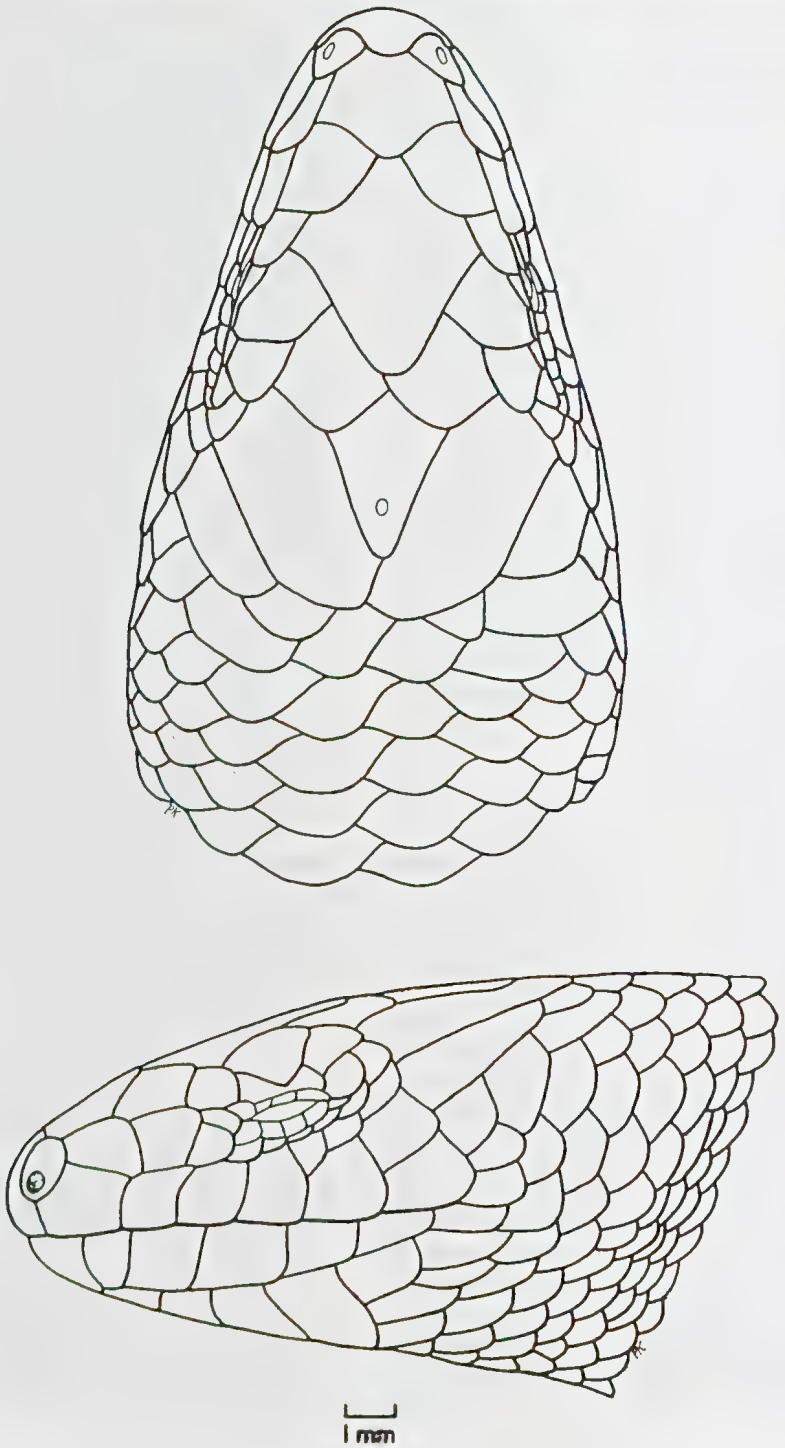

Fig. 39. Head of *Coeranoscincus frontalis* (CAS 44130).

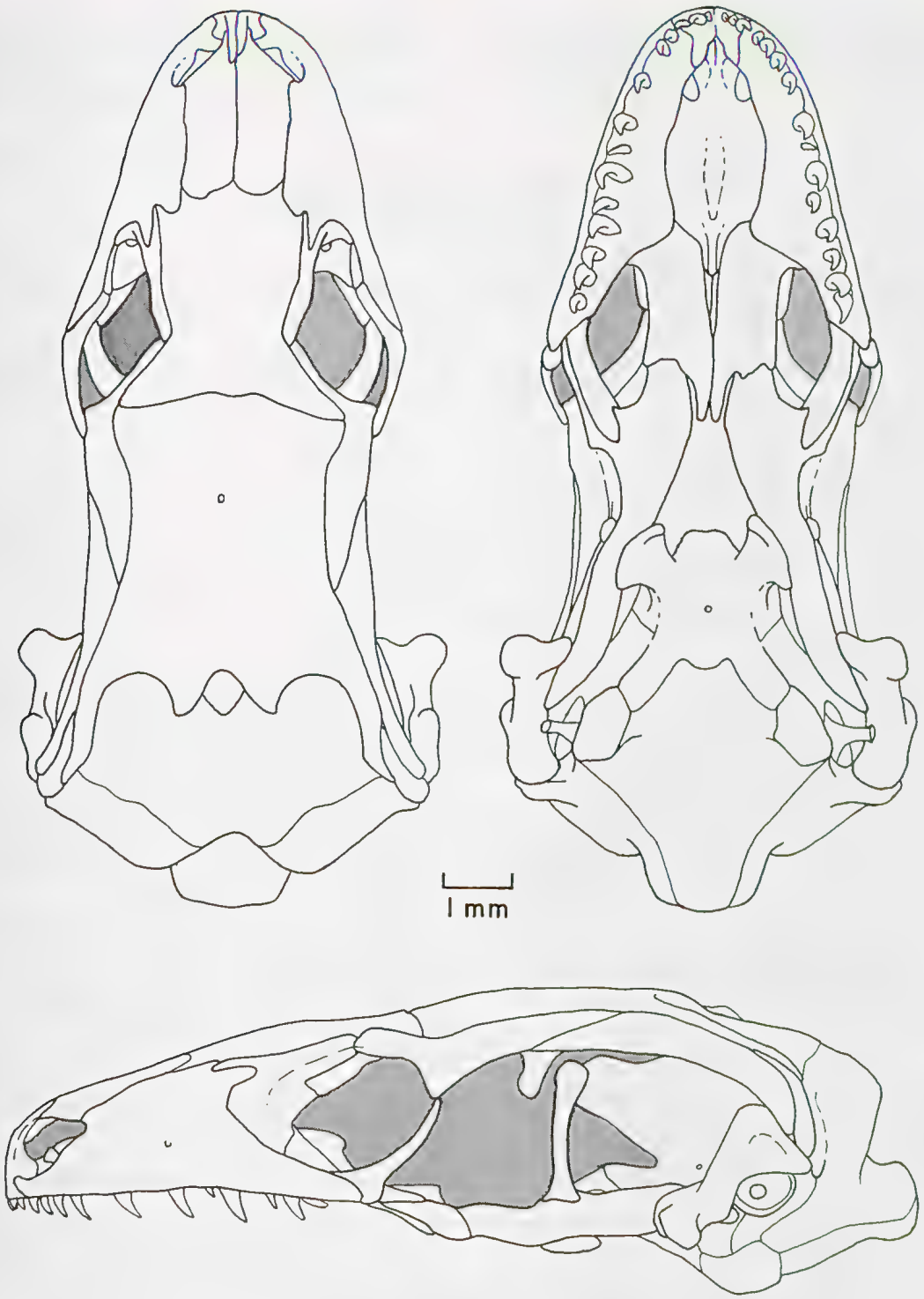

Fig. 40. Skull of *Coeranoscincus frontalis* (AM R 3823).

C. frontalis the pectoral girdle is highly modified: the clavicles are thin and rod-like; the interclavicle is absent; the sternum is assymetrical and more rectangular than rhomboidal; only one rib (from ninth presacral vertebrae) contacts the sternum and there is no mesosternum.

The **rear limb** is tridactyl with a phalangeal formula of 0.2.3.3.0 in *C. reticulatus* but is totally absent in *C. frontalis*.

The distal ends of the **sacral diapophyses** are in broad contact in *C. reticulatus* but separated in *C. frontalis*.

The **pelvic girdle** conforms to the primitive scincid condition in *C. reticulatus* but is reduced to a blade-like ilium with attached scale-like vestiges of the pubis

and ischium in *C. frontalis*.

In most of the characters in which the two species of *Coeranoscincus* differ, and which can be fairly assessed in terms of primitive and derived character states (above and Table 8), *C. reticulatus* is more primitive and *C. frontalis* more highly derived. The only exceptions are the prefrontals, secondary temporals, palate and surangular; in these, *C. frontalis* is more primitive.

Key to Skink Genera in Australia with Species Having a Reduced Number of Digits

1. Outer preanal scales overlap inner; digital formula 4–5 2
——Inner preanal scales overlap outer; digital formula 4–4 or less 5
2. Lower eyelid moveable 3
——Lower eyelid a spectacle ..... *Menetia*
3. Prefrontals present 4
——Prefrontals absent ..... *Anotis*
4. Frontoparietals distinct ..... *Saproscincus*
——Frontoparietals fused ..... *Carlia*
5. External ear opening present ..... *Lerista*
——External ear opening absent 6
6. Lower eyelid scaly 7
——Lower eyelid with a clear window ..... *Hemiergis*
7. Ectopterygoid process present 8
——Ectopterygoid process absent 9
8. Digital formula 3–3; premaxillary teeth 8–9 ..... *Saiphos*
——Digital formula 3–2 or less; premaxillary teeth ⩽ 7 ..... *Anomalopus*
9. Supralabials 6, fourth subocular; frontal in contact with 2 (of 3) supraoculars. ..... *Coeranoscincus*
——Supralabials 5, third subocular; frontal in contact with only 1 (of 3) supraoculars. ..... *Ophioscincus*

Key to Limbless Species of Lygosomine Skinks

1. External ear opening present (although minute) 2
——External ear opening absent 3
2. Eye covered by moveable eyelid ..... *Lerista ameles*
——Eye covered by fixed ocular scale ..... *Lerista apoda*
3. Supralabials 6 4
——Supralabials 5 or fewer (4% of *A. gowi* have 6) 7
4. Nasal and first supralabial scale distinct 5
——Nasal and first supralabial scale fused ..... *Anomalopus* (*Vermiseps*) *pluto*
5. Paravertebral scales 84–138; size smaller, maximum SVL 107 mm 6
——Paravertebral scales 151–197; size larger, maximum SVL 291 mm. ..... *Coeranoscincus frontalis*
6. Midbody scale rows 22–26; supraciliary scale row continuous; loreals usually 2 (8% with 1) ..... *Anomalopus* (*Vermiseps*) *swansoni*

——Midbody scale rows 18–20; supraciliary scale row interrupted (last supraciliary separated from anterior supraciliaries by last 1 or 2 supraoculars); loreal one. ..... *Anomalopus* (*Vermiseps*) *brevicollis*

7. Prefrontal present 8

——Prefrontal absent 10

8. Loreals 2 ..... *Ophioscincus ophioscincus*

——Loreals 1 9

9. Midbody scale rows 22–26; supraciliary scale row continuous; pretemporal 1; a distinct dark lateral stripe; Asia ..... *Isopachys anguinoides*

——Midbody scale rows 18–20; supraciliary scale row interrupted (last supraciliary scale separated from anterior supraciliaries by last 1 or 2 supraoculars); pretemporals 2; no distinct dark lateral stripe; Australia. ..... *Anomalopus* (*Vermiseps*) *gowi*

10. Supralabials 5; frontonasal distinct 11

——Supralabials 4; frontonasal not distinct ..... *Isopachys gyldenstolpei*

11. Frontoparietals in contact; pretemporals 2; mental and postmental distinct; Australia ..... *Ophioscincus cooloolensis*

——Frontoperietals separated; pretemporal 1; mental and postmental fused; Asia. ..... *Isopachys roulei*

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Table 1. Comparison of certain characters in the three species of the subgenus *Anomalopus* of the genus *Anomalopus*.

Character	*A. mackayi*	*A. verreauxii*	*A. leuckartii*
Digits	3–2	3–1	2–1
Midbody scale rows			
Range	18–20	18–23	18–22
$\bar{x}$	19.1	20.1	20.8
Mode	20	20	20
SD	1.03	0.74	0.99
N	14	37	56
Paravertebrals			
Range	97–116	110–129	108–128
$\bar{x}$	104.8	118.2	117.2
SD	5.45	4.66	5.04
N	13	25	19
Number of supraoculars			
4	1.00	0.91	0.75
3	–	0.09	0.23
2	–	–	0.02
N	11	46	62
Supraciliaries			
Range	6–7	6–7	5–7
$\bar{x}$	6.8	6.8	6.1
Mode	7	7	6
N	13	35	96
Transversely enlarged nuchals			
Range	0–1	0–2	0–4
$\bar{x}$	0.1	0.2	0.2
Mode	0	0	0
N	14	42	74
Snout-vent length (mm)			
Range	63–123	44–185	39–137
N	13	143	120
Length of front leg/ snout-vent length			
Range	0.05–0.07	0.03–0.06	0.03–0.04
N	12	23	18
Length of rear leg/ snout-vent length			
Range	0.04–0.08	0.01–0.03	0.01 or less
N	12	23	2
Tail length/ snout-vent length			
Range	1.03–1.21	0.98–1.40	0.69–1.24
N	2	37	43
Presacral vertebrae			
Range	51–58	53–57	51–55
$\bar{x}$	53.9	54.7	52.8
SD	2.26	1.40	1.11
N	9	31	16

Table 1. continued

Character	*A. mackayi*	*A. verreauxii*	*A. leuckartii*
Postsacral vertebrae			
Range	–	57–62	50–54
$\bar{x}$	–	57.7	52.0
SD	–	1.49	1.63
N	–	11	4
Complete inscriptional chevrons			
Range	11–13	12–14	10–14
$\bar{x}$	11.8	13.1	11.8
N	4	12	16
Sternal/mesosternal ribs			
3/2	–	0.08	–
2/2	1.00	0.92	0.86
2/1	–	–	0.14
N	2	12	14

Table 2. continued

Character	*A. swansoni*	*A. pluto*	*A. gowi*	*A. brevicollis*
Number of supralabials				
6	1.00	1.00*	0.04	1.00
5	–	–	0.96	–
N	38	6	24	39
Frontoparietals				
Meet	1.00	–	0.20	0.97
Separate	–	1.00	0.80	0.03
N	43	5	25	38
Transversely enlarged nuchals				
Range	0	1–2	1–4	1–4
$\bar{x}$	0	1.3	3.2	3.2
Mode	0	1	3	3
N	40	6	28	39
Infralabials contacted by postmental				
2	1.00	–	1.00	0.93
1	–	1.00	–	0.07
N	3	5	25	42

*Based on inference that first supralabial is fused to nasal

Table 2. Comparison of certain characters in the four species of the subgenus *Vermiseps* of the genus *Anomalopus*.

Character	*A. swansoni*	*A. pluto*	*A. gowi*	*A. brevicollis*
Midbody scale rows				
Range	22–26	22–23	18–20	18–20
$\bar{x}$	23.6	22.2	19.0	18.4
SD	0.95	0.45	0.99	0.76
N	34	5	25	47
Paravertebrals				
Range	115–138	126–136	105–117	84–102
$\bar{x}$	128.7	131.0	111.9	90.3
SD	7.12	3.90	3.81	4.73
N	14	6	24	41
Number of supraoculars				
4	–	–	–	–
3	0.81	–	–	0.95
2	0.19	1.00	1.00	0.05
N	37	6	25	39
Number of supraciliaries				
5	0.05	–	–	–
4	0.95	–	0.96	0.05
3	–	1.00	0.04	0.95
N	44	6	25	41
Number of loreals				
2	0.97	1.00	–	–
1	0.03	–	1.00	1.00
N	37	7	25	39

Table 3. Distribution of character states used to infer the phylogenetic relationships of the four species of the subgenus *Vermiseps*. Primitive character states are indicated by an upper case letter, derived states by lower case letters and, if necessary, superscripts. If a character varies intraspecifically, only the most primitive character state is entered.

Character	ancestor	*A. swansoni*	*A. pluto*	*A. gowi*	*A. brevicollis*
Nasals separated (A) or in contact (a)	A	A	A	a	a
Prefrontals present (B) or absent (b)	B	B	B	b	b
Supraoculars 4 (C) or 2 (c)	C	C	c	c	C
Posterior supraocular excluded from supraciliary row (D) or entering it (d)	D	D	d	d	d
Supraciliaries 5 (E) or fewer (e)	E	E	e	e	e
Posterior loreal present (F) or absent (f)	F	F	f	f	f
Subocular scale row large (G) or much reduced (g)	G	G	g	g	g
Infralabials 5 (H) or 4 (h)	H	H	h	h	H
Premaxillary teeth 7 (I) or ≤6 (i)	I	I	i	i	i

Table 3. continued

Character	ancestor	*A. swansoni*	*A. pluto*	*A. gowi*	*A. brevicollis*
Frontal's ventral processes weak (J) or moderate to strong (j)	J	j	J	j	j
Fenestra rotunda moderate in size (K) or reduced to small foramen (k)	K	k	K	k	k
Sacral diapophyses fused (L) or separate (l)	L	l	L	l	l
Pubes present (M) or absent (m)	M	M	m	m	m
First supraciliary separated (N) or in contact (n) with frontal	N	N	n	n	n
Parietal peritoneum pigmented (O) or not (o)	O	o	o	O	O

Table 4. A comparison of certain characters among the three species of *Ophioscincus*.

Character	*O. truncatus*	*O. cooloolensis*	*O. ophioscincus*
Midbody scale rows			
Range	18–22	18–19	20–24
$\bar{x}$	19.6	18.1	21.7
Mode	20	18	22
N	39	13	37
Paravertebrals			
Range	77–90	77–83	94–113
$\bar{x}$	81.9	79.4	102.0
SD	4.08	2.23	5.28
N	9	12	13
Supraoculars			
3	1.00	0.69	0.66
2	–	0.31	0.34
N	40	14	44
Number of loreals			
2	0.92	–	1.00
1	0.08	1.00	–
N	40	10	44
Transversely enlarged nuchals			
Range	1–7	2–5	0–4
$\bar{x}$	3.4	3.4	2.6
Mode	3	3	3
N	40	12	42

Table 4. continued

Character	*O. truncatus*	*O. cooloolensis*	*O. ophioscincus*
Number of infralabials			
5	0.36	–	–
4	0.64	1.00	1.00
N	28	11	22
Number of infralabials contacted by postmental			
2	0.92	0.92	–
1	0.08	0.08	0.98
0	–	–	0.02
N	40	12	43
Anterior pair of chin scales			
Contact	1.00	0.75	–
Separate	–	0.25	1.00
N	25	8	21
Snout–vent length (mm)			
Range	34–79	54–69	39–97
N	36	13	37
Tail length/ snout–vent length			
Range	0.71–0.95	0.77–0.93	0.59–0.88
N	32	3	22
Presacral vertebrae			
Range	45–50	43–44	49–51
$\bar{x}$	47.2	43.6	50.0
SD	1.07	0.55	0.68
N	32	5	14
Postsacral vertebrae			
Range	40–42	–	42
$\bar{x}$	41.1	–	–
SD	0.54	–	–
N	11	–	1
Complete inscriptional chevrons			
Range	12–15	11–12	14–16
$\bar{x}$	13.4	11.3	14.7
SD	0.92	0.52	0.87
N	8	6	9
Sternal/mesosternal ribs			
2/1	0.89	1.00	0.10
2/0	0.11	–	0.70
1/1	–	–	0.10
1/0	–	–	0.10
N	9	6	10

Table 5. Distribution of character states used to infer the phylogenetic relationships of the three species of genus *Ophioscincus*. Primitive character states are indicated by an upper case letter, derived states by lower case letters and, if necessary, superscripts. If a character varies interspecifically only the most primitive state is entered.

Character	ancestor	*O. truncatus*	*O. cooloolensis*	*O. ophioscincus*
Supraciliary row complete (A) or interrupted (a)	A	a	A	a
Posteromedial process of pterygoid weakly (B) or strongly (b) developed	B	b	b	B
Prefrontal and nasal bones in contact (C) or maxilla and frontal in contact (c)	C	c	c	C
Presacral vertebrae ≤ 44 (D) or ≥ 45 (d)	D	d	D	d
Front limb comprises a humerus, radial, ulna and one carpel (E) or only a humeral fragment or less (e)	E	E	e	e
Hind limb comprises femur, tibia and fibula and one tarsal (F) or only a femoral fragment or less (f)	F	F	f	f
Sacral diapophyses fused (G) or separated (g)	G	G	g	g
Ischia joined (H) or separated through reduction (h)	H	H	h	h

Table 6. A comparison of certain characters between the two species of *Coeranoscincus*.

Character	*C. reticulatus*	*C. frontalis*
Digital formula	3–3	0–0
Midbody scale rows		
Range	23–28	26–34
$\bar{x}$	26.0	29.7
SD	1.33	2.23
Mode	26	30
N	24	25
Paravertebrals		
Range	109–125	151–197
$\bar{x}$	116.3	178.6
SD	5.68	12.73
N	10	11
Supraoculars		
3	1.00	0.36
2	–	0.64
N	25	25

Table 6. continued

Character	*C. reticulatus*	*C. frontalis*
Digital formula	3–3	0–0
Supraoculars in contact with frontal		
2	1.00	0.36
1	–	0.64
N	25	25
Supraciliaries		
6	0.91	–
5	0.09	0.86
4	–	0.14
N	11	7
Transversely enlarged nuchals		
Range	2–4	0–2
$\bar{x}$	3.5	0.4
Mode	4	0
N	24	28
Snout–vent length (mm)		
Range	67–195	70–291
N	19	11
Tail length/ snout–vent length		
Range	0.98–1.47	0.47–0.57
N	7	6
Presacral vertebrae		
Range	52–55	72–76
$\bar{x}$	54.4	73.4
SD	1.06	1.41
N	8	8
Postsacral vertebrae		
Range	62+	38
$\bar{x}$	–	–
SD	–	–
N	1	1
Complete inscriptional chevrons		
Range	12–14	32–34
$\bar{x}$	13	33.0
N	2	2
Sternal/mesosternal ribs		
2/1	0.50	–
2/0	0.50	–
1/0	–	1.00
N	2	2

Addendum

Since this paper went to press a few changes and additions in our understanding of *Anomalopus leuckartii* and *A. verreauxi* have occurred. These are discussed below. The maps in the text (Figs 3 and 8) conform to these revisions.

Anomalopus verreauxi. Re-examination of QM J 11837 from 32 km N of Dayboro, Qld shows it to conform completely with *A. leuckartii.* It is therefore accepted as this species and the locality record rejected as being in error; there are no other records of *A. leuckartii* from the lowlands of far southeast Queensland (aside from the types of *Anomalopus lentiginosus*).

Additional specimens examined of *A. verreauxi* are: QNPWS R 58, 230, 578, 720-21, 724-25, 745, N 11381, 17670, 17759, 17924-25, 17670, 58799.

The furthest inland specimen is not QM J 37065 from Palm Gorge Fauna Reserve, Qld, but QNPWS N 10892 from Clemantis Creek, at the boundary between Glenaughton and Nugga Nugga Stations; this locality is approximately 250 km from the coast.

Anomalopus leuckartii. QM J 11837 is accepted as this species and not *A. verreauxi,* its locality of 32 km N of Dayboro, Qld is rejected as in error (see above).

Although the species appears not to occur in the lowlands of far southeastern Queensland, a specimen from Tamborine Mt., Qld (QM J 13935) may represent an isolated, high elevation population in this area.

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Marsupial Fossils from Wellington Caves, New South Wales; the Historic and Scientific Significance of the Collections in the Australian Museum, Sydney

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ABSTRACT. Since 1830, fossil vertebrates, particularly marsupials, have been collected from Wellington Caves, New South Wales. The history of these collections, and particularly of the collection housed in the Australian Museum, Sydney, is reviewed in this paper. A revised faunal list of marsupials from Wellington Caves is included, based on specimens in museum collections. The provenance of these specimens is discussed. The list comprises 58 species, of which 30 are extinct throughout Australia, and a further 12 no longer inhabit the Wellington region. The deposit also contains bones of reptiles, birds, bats, rodents and monotremes.

On the basis of faunal correlation and some consideration of taphonomy in the deposits, the age range of the fossils represented in the museum collections is suggested to be from the late Pliocene to late Pleistocene (with a possible minimum age of 40,000 years BP). Data from new collections indicate that at least three distinct periods of deposition are represented in the cave system.

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KEYWORDS: Australian, marsupials, Pleistocene, Pliocene, cave, fossils, history, Wellington Caves, Faunas, Australian Museum.

The Wellington Caves are about 8 km south of the town of Wellington on the Central Western Slopes of New South Wales (longitude 148° 51′ 30E, latitude 32° 31′S) in limestones belonging to the Devonian Garra Formation, at an altitude of approximately 300 m (Fig. 1). They occur in low hills 1 km east of the Bell River, at an elevation of about 50 m above the present stream. They comprise at least five natural caves which have been expanded and much disturbed in historic times by phosphate mining and fossil collection (Fig. 2). Vegetation of the area is tall open forest and the average annual precipitation for the area is about 630 mm, with a slight winter maximum.

These caves were the first known source of marsupial fossils in Australia and have proved to be one of the most prolific. Their significance stems from two main sources. The first is historic; early scientific descriptions of fossil bones constitute an essential background to taxonomic and phylogenetic studies of several groups of Australian marsupials. The second source of significance develops from the large quantity of fossil bones available, the great diversity of extinct species represented, and the likelihood that they represent at least three periods of deposition (Osborne, 1983).

Historical Background

The history of investigation of Wellington Caves and the fossils found in them, illustrates the philosophical development of the science of vertebrate palaeontology in Australia from its origins at the time of Cuvier, early in the 19th century, to the present day.

The discovery of the caves in the very early days of settlement of the western districts of New South Wales has been documented by Lane & Richards (1963). They give the earliest authenticated reference to the caves as that made by the explorer Hamilton Hume in December 1828. It is probable that they were known to Europeans several years before 1828. Augustus Earle, a colonial artist, who had travelled with Charles Darwin on the *Beagle*, visited the Wellington Valley in

Fig. 1. Map of the Wellington district of New South Wales. Small squares indicate fossil-bearing localities.

1826 or 1827 and sketched a cave then called Mosman's Cave (Hackforth-Jones, 1980), which was most likely the Wellington Cathedral Cave. The existence of the rich deposits of fossil bones in the caves was first reported in a letter from Mr George Ranken, a gentleman of Bathurst, to the Sydney Gazette of 25 May 1980 (Lane & Richards, 1963).

The early 19th century was a period of great interest in natural history and particularly in palaeontology. There was then almost universal acceptance of a "catastrophic" hypothesis as an explanation for the observed discrete stratigraphic distribution of extinct animal forms in the fossil record. The supposition that the Biblical Deluge was the last of such catastrophes inspired the interest of men of religion, as well as some scientists, both professional and amateur, in extinct animal remains.

In the young colony of New South Wales, two such men were the Surveyor General, Major Thomas Mitchell, a Fellow of the Geological Society of London, and the Reverend John Dunmore Lang, the colony's most prominent theologian. Both were acquainted with Mr Ranken, the discoverer of the Wellington Caves bones (Foster, 1936). Lang was instrumental in taking the first bones collected by Ranken to England for study by Professor Jamieson in Scotland in 1830 (Lane & Richards, 1963; Foster, 1936). Lang's interest was solely ecclesiastical and

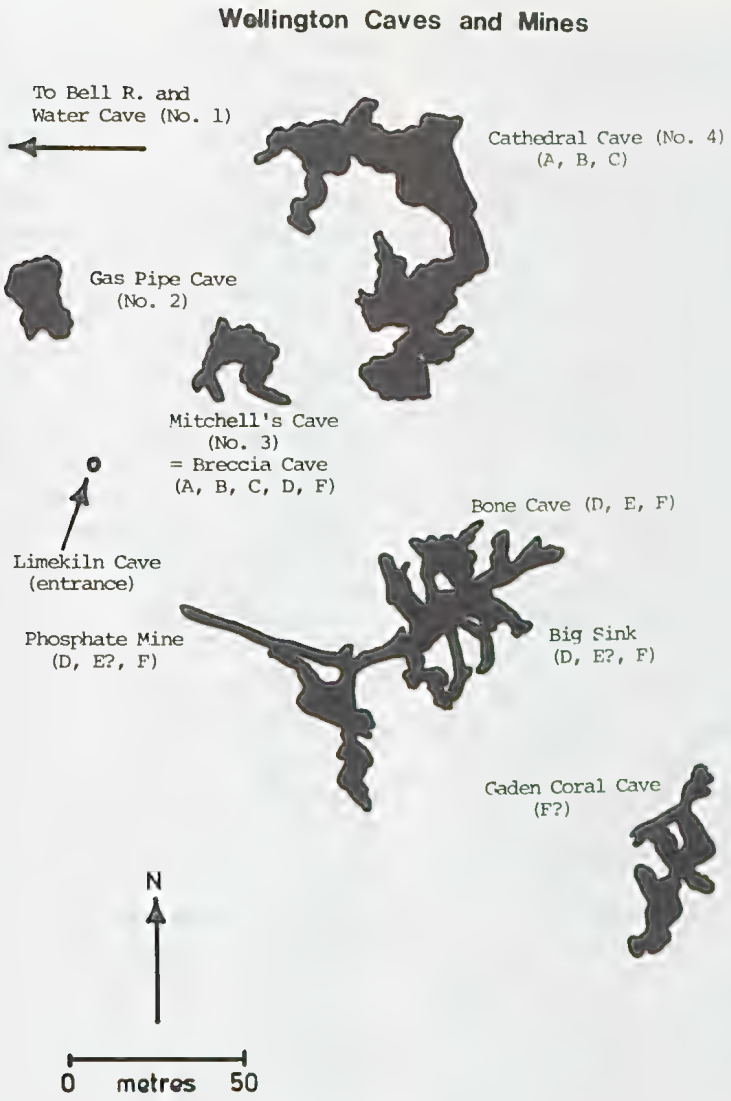

Fig. 2. Map showing the major caves and mines of the Wellington complex. From Frank (1971). Alternative cave names and numbers are shown. Letters A to F indicate the source of fossils in museum collections according to records of collectors as follows: **A**, Mitchell in 1830; **B**, Krefft in 1866, 1869; **C**, H. Barnes, for Ramsay in 1881; **D**, G. Sibbald for the New South Wales Department of Mines, from 1885 to 1909; **E**, Dr C. Anderson and colleagues from 1926 to 1932, **F**, L. Marcus in 1954.

aimed at finding evidence in the colony of the Biblical Deluge. Mitchell's interest was broader. Discoveries in the caves of Europe and England of human fossil bones with bones of extinct animals (Wendt, 1968) had led an English geologist, the Reverend William Buckland, to stress the importance of cave fossils in support of the Deluge hypothesis. Mitchell was well acquainted with the work of both Buckland and Cuvier. In 1829 he visited Bungonia Caves, New South Wales, with the chief aim (which was, however, unsuccessful) of finding "antediluvian remains, like those found by Mr. Buckland" (Foster, 1963: 434). With the same aim, Mitchell and Ranken visited the Wellington Caves and some other small caves in the Wellington Valley in July 1830, to make an initial survey of them and to collect fossil bones (Foster, 1936).

As a result, many more fossil bones were dispatched to England in the early 1830's to be examined by men of science in Scotland, Paris and England. At some time in 1831, Mitchell made a second collection of bones from the caves. These were sent to Paris for examination by Cuvier. Cuvier, however, died in 1832 and these bones were studied by his colleague, Mr William Pentland. Lane & Richards (1963) and Foster (1936) have given an extensive account of the movements of Mitchell's collections. The general ferment of ideas at the time, and the interest generated by the Wellington Caves bones is shown by the fact that Lyell, in his classic "Principles of Geology", published in 1833, referred to the bones collected by Mitchell as evidence supporting non-Cuvierian (i.e. evolutionary) principles (Owen, 1877: viii). Dugan (1980) has pointed out that the marsupial bones

discovered in Wellington Caves by Mitchell in 1830 probably provided the first inspiration for Charles Darwin's "Law of Succession of Types", formulated in 1837.

Sir Richard Owen, at that time Conservator of the Hunterian Museum of the Royal College of Surgeons, London, was the first to name extinct fossil marsupial species from Australia scientifically, on the basis of the bones from Mitchell's collection (Owen in Mitchell, 1838). The study of Australian fossil marsupials became a major part of Owen's life work. He published his last paper on a fossil from Wellington Caves in 1888, at the age of 84! Following receipt of Mitchell's first two collections, Owen received more bones from the Wellington Caves, sent to the Hunterian Museum in 1844 (see Flower, 1844) by the explorer Count Paul Strzelecki. By 1842 Owen's main source of Australian fossils was the Darling Downs of Queensland (Foster, 1936).

By 1866, independent scientific interest in the cave fossils was developing within Australia. Gerard Krefft, who had become Curator and Secretary of the Australian Museum in Sydney in 1861, made a large collection of fossil bones from the Wellington Caves, and sent them to the Paris Universal Exhibition of 1867 (Lane & Richards, 1963). In 1867, Owen requested that the Colonial Secretary of New South Wales grant 200 pounds for further exploration and collection from Wellington Caves (New South Wales Parliamentary Paper, 1882). This was granted and, in 1869, Krefft was directed to undertake the work. It is an indication of the developing maturity of the colony of New South Wales, and the independent attitude of Krefft, that most of the bones collected by Krefft in 1869 were not dispatched to England, but kept in the Australian Museum. Krefft sent Owen reports of his work in 1869 and 1870, accompanied by "duplicate" specimens, casts and photographs of some of the best specimens (*ibid.*, 1882). The specimens that remained in Sydney were, presumably, the first fossils from Wellington Caves to be lodged in the Australian Museum, although the collection was not registered immediately, and was not documented as to the exact origin of specimens.

Krefft's 1870 report to Owen was accompanied by a report from A.M. Thomson, Professor of Geology at Sydney University, describing the limestone of the Caves area and particularly Mitchell's Breccia Cave, from which Krefft's specimens were obtained. Thomson described the excavation of bone from Mitchell's Cave (i.e. Breccia Cave) and suggested that the caves may have originally been carnivore dens or had acted as pitfall traps for large animals (New South Wales Parliamentary Paper, 1882: 11–13). Krefft described several new genera and species (see Mahoney & Ride, 1975), and was particularly fascinated with the dentition of the Marsupial Lion, *Thylacoleo carnifex*. He disagreed publicly with Owen regarding the diet of this animal, considering *Thylacoleo* to have been herbivorous rather than carnivorous (Krefft, 1872a,b).

Two prolonged debates regarding the ancestry of man in Australia also stemmed from Krefft's discoveries in Wellington Caves. The discovery of the "Krefft tooth", a supposed human molar fragment, in the same breccia as the bones of extinct marsupial species, was claimed to be the first evidence for the antiquity of Aboriginal man in Australia, and for his coexistence with the "megafauna". However, no further evidence of man was ever found in the breccia. It was established by Campbell (1949) that the tooth was, in fact, not human, but a fragment of a macropodid premolar. Teeth of the Dingo, a placental species introduced by Aboriginal man to the Australian fauna, were also supposedly discovered by Krefft in the Wellington Caves fossil breccia. For nearly 100 years the contemporaneity of these teeth and the extinct species in the breccia was doubted. Gill & Sinnott (1973) demonstrated by a fluorine test that these Dingo teeth were, in fact, younger than bones of extinct species from Wellington Caves.

In 1874, Krefft was succeeded at the Australian Museum by Dr E.P. Ramsay, under whose leadership even more extensive collections were made from Wellington Caves. At the instigation of Sir Richard Owen and Sir George Macleay, the Agent General to the Colonial Secretary, funds were allocated to the Australian Museum in October 1876 for the further exploration of the caves of the western and southern districts of New South Wales, and to explore Australian rivers to collect endemic fish (New South Wales Parliamentary Paper, 1882). In June 1881, Ramsay dispatched Henry Barnes to collect fossils from Wellington Caves. Barnes, who had worked with Krefft at the caves in 1869, continued this work for five months. Ramsay wrote two extensive reports (*ibid.*, 1882) to the Trustees of the Museum on the progress of work at Wellington Caves. He was the first to identify the caves by number (see Fig. 2) and gave comparatively detailed information about the discovery of some of the fossil specimens. The many fossil bones excavated by Barnes and Krefft were stored in the Australian Museum, and comprise part of what is now referred to in the Museum fossil registers as the "Old Collection".

In 1884, the caves came under the control of the New South Wales Department of Mines, who engaged George Sibbald as the first keeper of the caves in 1885. Sibbald continued to work at the caves and collect fossils for 25 years until 1909 (Lane & Richards, 1963). Most of the fossils collected during this period were stored, unregistered, in the collections of the Geological and Mining Museum, Sydney.

By 1909, professional scientific interest in collection of fossils from the Wellington Caves virtually ceased. Between 1913 and 1917 the New South Wales Phosphate Company mined the breccia-filled passages in the vicinity of the existing caves in search of phosphate for fertilizer. It is thought that the bone of the breccia which clogged these passages was the predominant source of phosphate (Frank, 1972: 80).

However, the phosphate source was probably not only bone, but phosphatic rim-rock (Osborne, 1983). Although many valuable specimens must have been exposed during the mining operations most, presumably, were crushed during extraction of the fertilizer.

The vast number of bones which comprised the Old Collections of the 19th and early 20th Century largely remained unsorted and unstudied until 1926, when Charles Anderson, another Director of the Australian Museum (1921–1940) revived interest in the Wellington Caves fossils (see Anderson, 1926, 1929). Some fossil specimens were sent to the Australian Museum early in 1926 by a Shire Clerk of Wellington, J. Harvey Truman, who had obtained them while electric lights were being installed in Cathedral Cave (Lane & Richards, 1963). Anderson and G. Clutton, of the Australian Museum staff, also collected fossils in 1926, mainly from the passages of the phosphate mines (Anderson, 1926). In 1932, Anderson, accompanied by Mr W. Schevill of the Harvard University Museum of Comparative Zoology, again visited the caves and made an extensive collection from the phosphate mine passages (Anderson, 1932)

Anderson's interest resulted in the registration and identification of many of the specimens in the Old Collection. He was also responsible for the transfer of many previously unregistered specimens from the Geological and Mining Museum in Sydney to the Australian Museum in 1930, 1934 and 1935 (see the MF register of the Australian Museum). In 1939, German scientists made a large collection from the Bone Cave, Mitchell's Cave and the Phosphate Mines (Schroeder & Dehm, 1940; Dehm & Schroeder, 1941). These authors report collecting a large range of species, both large and small. This collection was eventually shipped to Munich, where it presumably remains in the Institute for Palaeontology and Historical Zoology. The collection has not been described. The best documented recent collection from the caves was made by L.F. Marcus in 1954, and is deposited in the University of California Museum of Paleontology (UCMP Accession number 1601).

Current Scientific Significance

The large collections from Wellington Caves, which have accumulated over 150 years, represent an important source of information about many extinct marsupial species. One hundred Australian fossil marsupial species names were proposed between 1838 and 1900 (Mahoney & Ride, 1975). Of these 23 are attributed either definitely, or probably, to Wellington Caves as the type-locality. Until the present study, most of these taxa were in need of revision. A further 54 fossil species were named from the other "classic" locality, the Darling Downs region of Queensland. These deposits were both assumed by 19th century workers to be of Pleistocene age. As recently as 1933, Charles Anderson wrote that "information regarding Tertiary marsupials is almost a blank" (Anderson, 1933: xxi). At that time only one Tertiary species, *Wynyardia bassiana*, was known.

This lack of an older record probably contributed to the waning of general interest in marsupial palaeontology in the first 50 years of this century. Intensive effort to discover Tertiary marsupials in Australia was pioneered by R.A. Stirton in the early 1950's. Initial modest success (e.g. Stirton, 1955, 1957) rapidly rekindled interest, and led to a progressively more intensive phase of exploration. This resulted in discovery of Tertiary representatives of most Australian marsupial families (excluding only the Tarsipidae, Myrmecobidae and Notoryctidae) extending back, in most cases, as far as the early Miocene (15 million years BP) (Archer & Bartholomai, 1978).

In 1964, W.D.L. Ride stressed the need for "rediscovery" and reinterpretation of the classic fossil localities and faunas. In fact, such work was then already underway in Queensland, where Woods (1960) had established the presence of two distinct stratigraphic units and two faunas within the Darling Downs region. He designated the eastern Darling Downs fluviatile deposits as Pleistocene in age and presumed the older unit, the Chinchilla Sand, to be late Pliocene or early Pleistocene age. Revision of fossil taxa from these Queensland fossil faunas has been the subject of many papers by Bartholomai over the past 20 years (e.g. Bartholomai, 1963, 1970, 1973, 1975, 1976). The Chinchilla Sand is now considered to be early to middle Pliocene in age (Rich *et al.*, 1982).

The Wellington Caves also rank as one of the classic localities in Australia for marsupial fossils, and hence deserve similar revisionary study and renewed investigation. Recent geological studies have shown that the deposit is undoubtedly not stratigraphically homogeneous (Frank, 1971, 1972, 1975; Francis, 1973; Osborne, 1983). These studies have suggested the probability that the bone-bearing breccia represents at least three periods of deposition, probably ranging from the Pliocene to the late Pleistocene (Osborne, 1983). This geological hypothesis has formed the basis for a new stratigraphically controlled analysis of the fossils, currently being undertaken through the School of Zoology, University of New South Wales.

Results of that study are not yet available. However, a preliminary study involving revision of the existing museum collections has been undertaken (Dawson, 1982a). The background to, and some results of, that study are reported here.

Revision of Museum Collections from Wellington Caves

The large number of specimens from Wellington Caves in the Australian Museum and other institutions has provided an opportunity to investigate the validity of several fossil taxa, and to study variation in extinct species described from this location and elsewhere in Australia. Another aim of the revision of museum

collections was to establish the range of species present in the deposit. It was hoped that this preliminary study would enable use of faunal correlation to test the geological hypothesis as to the age range of the deposits.

The value of faunal correlation in estimating the relative age of Australian fossil deposits has recently been stressed by Archer (1978) and Rich *et al.* (1982). A preliminary requirement is an understanding of the range of variability within species, and consequent understanding of the morphological boundaries of each species.

For historic and biogeographic reasons, studies of fossils from the Queensland Darling Downs are of particular importance for stratigraphic correlation and palaeoecological interpretation of the Wellington Cave fossils. Other studies of particular relevance, because of the geographic relationship of the deposits to Wellington Caves, are of the Pleistocene faunas of Lake Menindee (Tedford, 1967), Bingara (Marcus, 1976), Lake Victoria region (Marshall, 1973), and Lake Tandou (Merrilees, 1973) in New South Wales; and of Texas Caves (Archer, 1978), and Gore (Bartholomai, 1977) in Queensland. Similar faunal studies relevant to the development of an Australia-wide picture of Pleistocene marsupials are those of Marshall (1974) on the Keilor "cranium site", and Gillespie *et al.* (1978) on Lancefield Swamp in Victoria; Hope *et al.* (1977) on Seton Rock Shelter, Kangaroo Island, Williams (in Wells, 1978) on Dempsey's Lake, and Smith (1971, 1972) and Wells and colleagues (as yet largely unpublished) on the fauna of Victoria Cave, Naracoorte, South Australia; Murray & Goede (1977) on Tasmanian caves; and Baynes *et al.* (1975) and Balme *et al.* (1977) on Devils Lair, and Merrilees (1968) on Mammoth Cave, Western Australia.

Certain eastern Australian deposits containing rich marsupial faunas are known, by potassium-argon dating and by the level of phylogenetic development of taxa in them, to be of Pliocene age (see Rich *et al.*, 1982, for a summary of the age of Tertiary marsupial faunas). Those of most relevance for comparison with the Wellington Caves assemblage are the Chinchilla Sand local fauna of southeastern Queensland (approximately 4 million years BP based on stage of evolution), the Bow local fauna, New South Wales (approximately 4 millions years BP based on stage of evolution), the Hamilton local fauna, Victoria (4.3 million years BP, radiometric dating) and the Bluff Downs local fauna, Queensland (4.5 million years BP based on radiometric dating).

Problems of Provenance

There are fossil specimens from Wellington Caves in museums and private collections throughout Australia and much of the world. The largest collectons are in the Australian Museum, Sydney, the British Museum (Natural History), London, and the University of California Museum of Paleontology, Berkeley. The present study has involved all three of these collections, with most emphasis on the Australian Museum collection. In many cases the documentation of the museum specimens is poor. The problem of provenance of these museum specimens exists on three levels: (1) confirmation of the origin of a specimen from any one of the Wellington Caves (see Fig. 2), (2) identification of the particular cave or fissure of origin of a specimen and (3) identification of the geological strata from which a specimen originated.

Although Frank (1971) and Osborne (1983) have identified at least three stratigraphically distinct bone-bearing units in the clastic fill of the Wellington Caves, no specimen in existing museum collections is labelled as to the stratigraphic unit of its origin. Frank (1971, 1975) found that the highest bone density was in the ubiquitous units which he designated 3R and 3RB, and that these contained bones of the largest animals. It is likely, therefore, that the majority of bones in existing collections have come from these units.

Some museum specimens are accompanied by relatively detailed information as to their origin. In the collections of L.F. Marcus in the University of California Museum of Paleontology, Berkeley, each specimen is accompanied by a locality number indicating the particular cave of origin. In the Australian Museum collections 47 specimens (AM F31012–F31057), collected by C. Anderson and W. Schevill in February 1932, originate from "... the drives put in some years ago by a Phosphate Company in search of fertilizer..." (Anderson, 1932). Similarly, 25 specimens (AM F18896–F18920), collected by C. Anderson and G.C. Clutton in 1926, probably all originated from "...the passages driven into the hill by the Phosphate Company..." (Anderson, 1926: 369). A further eleven specimens (AM F18658–F18870) were collected in one of the caves (probably Cathedral Cave) by a Shire Clerk of Wellington, J. Harvey Truman, early in 1926 (Anderson, 1926: 368). In all, 57% of the total number of marsupial species identified here from Wellington Caves are represented in these relatively well documented collections.

The provenance, at Wellington Caves, of specimens collected prior to 1926 is more difficult to authenticate, although it can be established that they are derived from four major collection episodes. These are (1) the first collections by Mitchell in 1830, 1831; (2) the collections of Krefft in 1866, and Krefft and Thomson in 1869; (3) collections made by H. Barnes under the direction of Ramsay in 1881; and (4) collections made between 1885 and 1917, while the caves were under the control of the New South Wales Department of Mines. Those made prior to 1884 were probably all from Cathedral Cave and Mitchell's (Breccia) Cave.

Specimens which were sent to the British Museum are listed by Lydekker (1887). Most originate from the

collections of Krefft (who mentions, in his 1870 report, the dispatch of 1000 specimens!) and Barnes (under Ramsay). Their detailed reports (New South Wales Parliamentary Paper, 1882: 4, 8, 44, 45) confirm the origin of the specimens from Cathedral Cave or Mitchell's Cave.

The British Museum collections also include those specimens collected by Sir Thomas Mitchell in 1830 and 1831. Problems relating to the exact provenance of these specimens have been discussed by Mahoney & Ride (1975: 33, 34). These authors have concluded that it is not possible to exclude an unnamed site "...on the north bank of the Macquarie, 8 miles east of Wellington Caves", nor the caves at Buree (= Tunnel Cave, Borenore) as the possible source of some of Mitchell's specimens. However, Frank (1972), in a study of the Borenore Caves, has noted that very little bone or organic material is present in this deposit. From Mitchell's (1838) description, it is clear that Wellington Caves, and particularly the Breccia Cave, were the source of most of the specimens that were sent to England.

The majority of the specimens in the Australian Museum, labelled as coming from Wellington Caves, bear the designation "Old Collection". These were collected prior to August 1887, when the current system of registration (F registers) commenced. They were registered, sporadically, from 1897 onwards. A few bear corroborative information as to their provenance, e.g. F4643, "*Diprotodon* ulna, Wellington Caves, Cave 3, Collected H. Barnes".

Transfer of specimens from the Geological and Mining Museum, Sydney, to the Australian Museum took place in October 1930, then in 1934, 1935 and 1939, to be registered in the Australian Museum under the prefix MF. Many more specimens were transferred in 1963, 1964, 1968 and 1976 (see Australian Museum F register). There are no records available as to the detailed provenance of most of these specimens, other than the designation "Wellington Caves". However, it is probable that they were collected between 1884 and 1917, the period during which the Caves were under the control of the New South Wales Department of Mines. Some bear corroborative information regarding their origin from the Wellington Caves, e.g. MF 465 (old no. 1389), "macropod lower incisor, Collected J. Sibbald, Cave No. 3, Wellington".

It is possible that some of the specimens from the Mining Museum were mislabelled prior to their transfer to the Australian Museum. For those specimens without any other documentation as to their origin, the state of preservation provides the best supporting evidence for origin from one of the Wellington Caves. Of the taxa listed in Table 1, five species are only represented by single specimens from the old Mining Museum collections. These are *Phascolonus gigas* (MF728/9), *Thylogale* sp. (MF304), *Macropus* sp. cf. *M. giganteus* (MF124), *Macropus* sp. cf. *M. dryas* (F47077e) and *Macropus* sp. cf. *M. rama* (F47115). All other taxa included among the specimens transferred from the Mining Museum are also represented in various other better documented collections from Wellington Caves.

Examples have been found indicating that some mislabelling of museum specimens has probably occurred, e.g. (1) AM F1063, "*Macropus* maxillary fragment", a specimen similar in preservation to those known to come from Wellington Caves, is labelled "Cave Flat, Murrumbidgee, collected Jenkins", but bears the letters "W.C." in black ink on the specimen; (2) AM F30330, the holotype of *Halmaturus thompsonii* Krefft, 1870 was registered in 1931. Mahoney & Ride (1975) give Wellington Caves as the probably type-locality for this species. However, the preservation of the holotype is unlike any other known to come from Wellington Caves, and is, in fact, typical of specimens from the Darling Downs, Queensland. It is thus considered here to have been wrongly labelled at the time of registration.

Specimens known to originate from Wellington Caves vary in colour, degree of mineralisation, and in the hardness and colour of any adhering matrix. The observed variety of preservation states is typical of fossils from cave earth and cave breccia from several localities. Thus, specimens indistinguishable in preservation from Wellington Caves specimens are known from Molong (e.g. AM F31734) and from Guerie, 16 km north of Wellington (e.g. AM F41457, collected by Robertson and Fletcher, 1944). Preservation alone, therefore, is not an infallible guide to a specimen's origin from Wellington Caves.

Unfortunately a degree of uncertainty will always remain as to the exact provenance of many specimens from the "Old Collections" in the Australian Museum. It is clear, however, from the history of the caves and the documentation available, that only a small proportion of the total collection is likely to be mislabelled as to locality. This study has proceeded on that assumption.

Marsupials from Wellington Caves

The marsupial taxa represented in Museum collections from Wellington Caves are listed, with annotations, in Table 1. This faunal list has been compiled after study of specimens in the collections of the Australian Museum, Sydney, the British Museum (Natural History), London, and the Museum of Paleontology, University of California, Berkeley. At least one representative specimen from a museum collection is nominated for each species. Where possible, these examples have been chosen because they are accompanied by documentation supporting their origin from the Wellington Caves. For most species, corroborative evidence of occurrence in one of the Wellington Caves has been obtained from new collections made by the author and colleagues from the University of New South Wales in 1983 and 1984, as noted in Table 1.

In many cases the origin of a specimen from a

specific cave in the system is documented. In other cases only the name(s) of the collector(s) is known. This is taken as corroboration of origin from Wellington Caves where it is established that this was the only location worked by that person (e.g. Anderson & Schevill in 1932).

In most cases a detailed comparative morphometric study has been undertaken for each species. Some results of these studies have been published; on thylacines (Dawson, 1982c), on Tasmanian Devils, *Sarcophilus* spp. (Dawson, 1982b), on the Marsupial Lion, *Thylacoleo carnifex* (Archer & Dawson, 1982) and on wombats (Dawson, 1981, 1983a,b). Detailed studies of the macropodids have also been undertaken but are yet to be published (see Dawson, 1982a).

Two of the mammalian species which Mahoney & Ride (1975) attribute to Wellington Caves are considered here to be *nomina dubia*. These are *Osphranter gouldii* Owen, 1874, and *Hypsiprymnus spelaeus* Waterhouse, 1845. In each case the holotype was destroyed when the Royal College of Surgeons, London, was bombed in 1941 (see Mahoney & Ride, 1975). A neotype cannot be assigned to either of these names since no specimens other than the holotype have been referred to either species, and the original descriptions are inadequate to assign any specimen to either of these taxa.

Non-marsupial Vertebrates from Wellington Caves

Reptiles. Numerous small reptilian jaw fragments are represented in the Australian Museum collections, both old and new, from Wellington Caves. Few have been registered, and they remain entirely unstudied. Most represent agamids and varanids. The giant varanid, *Megalania prisca*, is also present in the fauna, being represented by several postcranial fragments, including a dorsal vertebra, AM F16494. A portion of a carapace, AM F18662, represents a turtle or tortoise in the fauna. It is probably the specimen mentioned by Thompson (New South Wales Parliamentary Papers, 1882), found in Mitchell's Cave.

Birds. Rich (1975) notes the following fossil birds from the Wellington Caves: *Dromaius patricus* (? *D. novaehollandiae*, Casuariidae, emu); Dromornithidae (mihirung bird); *Progura gallinacea* (Megapodiidae, mound builder); *Casuarius lydekkeri* (Casuariidae, cassowary). Lydekker (1891a) first claimed the existence of a fossil cassowary from the Pleistocene of New South Wales, after examination of a cast in the British Museum. Rothschild (1911) based his description of *C. lydekkeri* on this cast (BM A158 or B10394), claiming that it was from the Queensland Pleistocene. Miller (1962) confirmed that this cast is from a distal end of a tibiotarsus, MF 1268, a specimen in the Australian Museum. This specimen was transferred to the Australian Museum from the Mining Museum, Sydney, in a tray of specimens of mixed origin (Miller, 1962). Miller (1962), following H.O. Fletcher, concluded that this specimen came from Wellington Caves. After examination of the specimen, I have concluded that this is very unlikely, on the basis of its preservation. The greenish colour of the bone is quite unlike any specimen known to come from Wellington Caves, but not unlike specimens from the eastern Darling Downs. It is concluded here that this species should not be included in the Wellington Caves fauna.

In May 1984, Tim Flannery of the School of Zoology, University of New South Wales, collected a tibio-tarsus in the Bone Cave which is probably from a species of *Genyornis* (P. Rich, pers. comm., 1984).

Monotremes. Murray (1978) has confirmed the identity of a fossil echidna, *Zaglossus ramsayi* Owen, 1844, the holotype of which (AM F10948) was obtained by E.P. Ramsay from the Breccia Cave (No. 3), Wellington Caves. This species has also been reported from Pleistocene deposits of Henschke's Cave, South Australia; King Island and Montagu Caves, Tasmania; and from Mammoth Cave, Western Australia (Murray, 1978; Pledge, 1980).

Rodents. Rodent jaws are abundant in new collections from Wellington Caves but these have not as yet been described. They are particularly abundant in the Bone Cave. A new genus and species, *Paraleporillus stirtoni* Martinez & Lidicker, 1971, has been described on the basis of a specimen from the Bone Cave. The holotype was collected by L.F. Marcus in 1954. This species is considered by Watts & Aslin (1981) to be a junior synonym of *Pseudomys australis*.

Bats. *Macroderma gigas*, the Ghost Bat, has been reported from an unknown locality in Wellington Caves by Molnar *et al.* (1984). Additionally, skulls and jaws of a new, more primitive species of Ghost Bat, possibly ancestral to *Macroderma gigas* (S. Hand, pers. comm. 1984) have been isolated from breccia from the Big Sink, collected by Michael Archer and students in 1982.

Discussion

The faunal assemblage from Wellington Caves contains a very high proportion (65%) of extinct or gigantic marsupial species, most of which are also typically found in other Pleistocene-aged faunas of eastern Australia (e.g. the eastern Darling Downs, Queensland, and Bingara, New South Wales). However, geological evidence suggests that a component of the Wellington deposits could predate the Pleistocene (Osborne, 1983).

Although, faunally, the Pliocene/Pleistocene boundary itself is not yet defined, a clear faunal difference can be seen between the better documented earlier Pliocene faunas, and those of middle or late Pleistocene age. Thus, among the diprotodontids, the presence of *Diprotodon optatum* and *Zygomaturus trilobus* only, supports a maximum age within the

Pleistocene, since neither of these species is known from a Pliocene deposit (Archer & Bartholomai, 1978; Archer, 1977). The most common palorchestid in Wellington Caves is *Palorchestes azael*, known only from Pleistocene deposits. The smaller species, *P. parvus*, once thought to occur only in the Pliocene (Woods, 1960), is now known to occur in the Pleistocene as well (Tedford, 1966; Bartholomai, 1977). Therefore, the occurrence of a species similar to *P. parvus* from Wellington Caves cannot be used to imply a greater stratigraphic range within the deposits.

Recent work has established the value of species of *Thylacoleo* in faunal correlation (Archer & Dawson, 1982). Thus, the Bluff Downs, Chinchilla Sand and Bow local faunas contain a large thylacoleonid (*Thylacoleo crassidentatus*) with dental features that are morphologically primitive compared to *T. carnifex*, the species typically found in Pleistocene deposits. The evidence available is most parsimoniously interpreted to indicate that evolution of the *T. crassidentatus–T. carnifex* lineage was orthogenetic. Progress along this morphocline is even suggested within the Pliocene by apparently different aged faunas, with *T. crassidentatus* from the older Bluff Downs fauna being structurally ancestral to *T. crassidentatus* from the younger Chinchilla Sand fauna (Archer & Dawson, 1982). Analysis of the larger number of specimens of *Thylacoleo* sp., in the museum collections from Wellington Caves, has shown that only one species, *T. carnifex*, is represented (Archer & Dawson, 1982). Specimens included in this analysis come from Bone Cave, Mitchell's Cave and Cathedral Cave. The results suggest that the period of deposition of these three units, although of unknown duration, was not long enough for significant evolutionary change to occur in this genus. Also, relatively large samples of *Thylacinus cynocephalus* and *Sarcophilus laniarius* from the same caves are not unduly variable (Dawson, 1982b,c) as could be expected if the samples represented a very long period of accumulation. It is concluded that the Museum collections do not contain a component local fauna of early or mid-Pliocene age, and probably represent deposits laid down from the early Pleistocene onwards.

Studies currently underway in the School of Zoology, University of New South Wales, now indicate that bones recently collected by the author and colleagues from the Big Sink from the upper member of the Phosphate Mine Beds (following the stratigraphy of Osborne, 1983) are of late Pliocene age. The unit is characterised by many specimens of a species of *Protemnodon*, tentatively assigned to *P. devisi*, a taxon previously known only from the Pliocene aged Chinchilla Sands of Queensland (Bartholomai, 1973), and by many specimens of a new, plesiomorphic species of Ghost Bat, genus *Macroderma*. This fauna will be described in a future paper. It is clearly derived from a stratigraphic unit of the Wellington Caves system which is not represented in the old museum collections.

Faunal considerations can also be taken into account in estimating the minimum age of the cave deposits, as represented by specimens in museum collections. The most recent review of evidence pertaining to the timing of extinction and dwarfing events of the late Pleistocene is that of Hope (1982). This suggests (a) that this was not synchronous throughout eastern Australia; (b) that the major episode occurred at or before 30,000 BP in inland areas, but that some giant taxa survived until approximately 20,000 BP in peripheral and particularly southern areas of the eastern continent; there is some evidence to suggest a few giant species survived until about 16,000 BP in Tasmania (Goede *et al.*, 1978) and on Kangaroo Island (Hope *et al.*, 1977); (c) that most extinctions and incidences of dwarfing occurred during a period which was wetter than the present, and predated the period of maximum aridity associated with the last glacial maximum, which occurred at approximately 18,000 BP (Bowler, 1980; Singh *et al.*, 1979). According to these hypotheses, and considering the geographic position of Wellington Caves, it would be expected that the major extinction event in that area occurred at least prior to 25,000 BP.

A particularly interesting aspect of the faunal assemblage from Wellington Caves is the almost complete absence of modern species of *Macropus*, even of the species of *Macropus* wallabies which are known from several faunas of late Pleistocene age elsewhere in Australia. At least ten species of *Macropus* are represented in the collections from the caves (see Table 1). All differ in some degree from modern species, although three modern species are represented by giant forms, here designated as subspecies. These are *Macropus giganteus titan*, *Macropus robustus altus* and *Macropus agilis siva*, all found in other sites of Pleistocene age throughout eastern Australia (Bartholomai, 1975). This almost complete absence of modern forms is similar to the situation found in the faunas of the eastern Darling Downs and Bingara, but contrasts with faunas of such localities as Naracoorte Caves, Cement Mills, Texas Caves, Lake Menindee, Lancefield Swamp and the Western Australian faunas of Devil's Lair and Mammoth Cave, all at least older than 20,000 BP (Hope, 1982). Each of these faunas contains at least one modern species; e.g. *M. rufogriseus* (Naracoorte, Lancefield, Lake Colongulac), *M. parryi* (Cement Mills), *M. dorsalis* (Cement Mills, Lancefield, Texas Caves), *M. rufus* (Lake Menindee, Dempsey's Lake), *M. eugenii* (Naracoorte Caves) and *M. greyi* (Naracoorte Caves). In Western Australia the fauna of Mammoth Cave, thought to have a minimum age of 37,000 BP (Archer *et al.*, 1980) contains *M. eugenii*, *M. irma* and *M. fuliginosus*. These same species occur throughout the well dated sequence from Devil's Lair to the lowest levels dated by carbon 14 at 31,000 BP

(Balme *et al.*, 1978). This apparent absence, in the Wellington Caves, of the most recently evolved group of modern species, therefore implies a minimum age definitely greater than 20,000 years BP, and probably greater than 37,000 years BP for the Wellington Caves bones.

Along with this faunal evidence, observations on the taphonomy of the bones must be taken into account in assessing the probable minimum age of the bone bearing deposits. The horizontal bedding and general taphonomy of bones in Unit 3RB (Frank, 1972; Obsorne, 1983) suggests that its minimum age (i.e. the time of its secondary deposition in that strata) coincides with a period when hydrological conditions were much wetter than now. There was evidently a much higher water table than now, or much ponding of water in the caves at the time of deposition of unit 3RB. However, that component of Frank's unit 3R, which is stratigraphically above unit 3RB, was deposited under much dryer conditions, at least as dry as the present (Frank, 1972). Collections made in 1983 by members of the School of Zoology, University of New South Wales, have established that this unit (3R) also contains predominantly large extinct species, at least where it occurs in the Bone Cave.

The work of Singh *et al.* (1979) and Bowler (1980) on the sediments of Lake George in the southern tablelands of New South Wales, and on the Mallee landforms of southwestern New South Wales, respectively, supports a hypothesis of prolonged periods of high water tables and full lakes in the late Pleistocene, punctuated by at least three arid periods, during which conditions were as dry as the present or dryer. These authors independently present evidence from different sources to suggest that lakes were full from at least 64,000 BP until approximately 22,000 BP, after which time conditions rapidly dried, reaching a period of maximum aridity much drier than at present at about 18,000 BP. As suggested above, the faunal evidence suggests a minimum age much greater than this last arid period. In fact, the combined faunas and stratigraphic evidence suggests that the arid period represented by unit 3R was not that of the most recent glacial maximum. According to Singh *et al.* (1979) and Bowler (1980), the last period of extensive aridity prior to that of 18,000 BP occurred at approximately 128,000 BP. Thus, although the evidence is far from conclusive, combined faunal, stratigraphic and hydrological information has suggested the tentative proposal here that the minimum age of the marsupial bones in the Wellington Caves (at least for bones from Bone Cave, Mitchell's Cave and the lower levels of the Cathedral Cave floor) could be near the end of the penultimate glacial, i.e. approximately 128,000 BP (Singh *et al.*, 1979; Bowler, 1980).

Conclusions

The systematic study of the museum collections from Wellington Caves involved revision of many fossil taxa described last century (Dawson, 1981, 1982a, 1982b, 1982c, 1983a, 1983b). Of the twenty-three fossil marsupial species listed by Mahoney & Ride (1975), for which Wellington Caves is the type-locality, or probably type-locality, only seven have been retained as full species. Nine have been synonymised with species described previously from other localities. One has been retained as a subspecies of a modern form. Two have been declared *nomina dubia* (Dawson, 1982a). The four diprotodontid species which are represented were not revised in this study. Additionally, at least three new genera, one a dasyurid and two macropodines, are represented in the collections. At least four new species of *Macropus* are represented (Table 1). These new taxa will be described in forthcoming papers by this author.

Wellington Caves fossils will continue to be of importance in comparative studies of faunas throughout eastern Australia because of the range of species represented. The large number of bones which remain unexcavated from the caves constitute a source of larger samples of those species which are, as yet, known from fragments only. Current excavations have revealed the caves to be an extremely rich source of many small species of marsupials and rodents. Some of these represent taxa which are, as yet, unrevised or undescribed.

One of the chief aims of current work at the caves is to obtain faunal data to corroborate the geological hypothesis of Osborne (1983), which suggests that at least three major periods of breccia deposition are represented in the Wellington Caves system. Early results of this new study, and the data presented in this paper, suggest that a fauna of mid to late Pliocene age is represented in the Big Sink. It is probable that the bone-rich deposits of Bone Cave and Mitchell's Cave, which were the source of most specimens in the old museum collections, accumulated during the Pleistocene (probably over a prolonged period), but that deposition in those caves probably ceased before the late Pleistocene. An important thrust of future work will be to obtain a more accurate estimate of the age of the bone in various stratigraphic horizons in the caves.

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Table 1. Marsupialia from Wellington Caves.

* Numbers prefixed by F- or MF- are Australian Museum specimens. Those prefixed by UCMP are from the University of California Museum of Paleontology; BM indicates specimens from the British Museum (Natural History).
(T) Indicates that Wellington Caves is the type-locality (or probable type-locality) of the taxon (see Mahoney & Ride, 1975).
O.C. Indicates a specimen from the "Old Collection" of the Australian Museum.
BC Indicates that the taxon is represented in collections made from the Bone Cave by Dawson and colleagues, 1983, 1984.
CC Indicates that the taxon is represented in collections made from the floor of Cathedral Cave by Dawson and colleagues, 1983, 1984.
BS Indicates that the taxon is represented in collections made from the Big Sink by Dawson and colleagues, 1983, 1984.

SPECIES		NOTES*
Marsupialia		
F. Thylacinidae		
Thylacinus cynocephalus		e.g. UCMP45183, coll. Marcus, 1954, from Phosphate Mine (V67189); F18660, coll. J. Harvey Truman, 1926; Presence of *Thylacinus* sp. from Breccia Cave noted by Krefft (1870). BC, CC, BS.
F. Dasyuridae		
Sarcophilus laniarius	(T)	e.g. F31045, coll. Anderson, 1932; UCMP45184, coll. Marcus, 1954 from Breccia Cave; UCMP45182 coll. Marcus, 1954 from Bone Cave. BC.
Dasyurus sp. cf. *D. maculatus*		e.g. F18897, coll. Anderson & Clutton, 1926. BC
Dasyurus sp. cf. *D. viverinus* or *D. geoffroi*		e.g. MF 144, exchanged Mining Museum, 1934. BC.
Phascogale tapoatafa		e.g. F62095, transferred from Mining Museum, ?1964. BS.
Phascogale sp.		e.g. F62103, transferred from Mining Museum, 1964. BC, CC.
Sminthopsis sp. cf. *S. murina*		e.g. F62097, transferred from Mining Museum, ?1964. CC, BC.
Antechinus sp. cf. *A. flavipes* or *A. stuartii*		e.g. F62098, transferred from Mining Museum, ?1964. CC, BC.
Genus indet.		e.g. F62110, F62113, transferred from Mining Museum, ?1964. BC.
F. Peramelidae		
Isoodon sp. cf. *I. obesulus*		e.g. F57920, O.C., CC, BC.
Perameles sp. cf. *P. nasuta*		e.g. BM43951, BM42639, presented to BM in 1870 (see Lydekker, 1887; Krefft, 1870); F57918. O.C., CC, BC.
Perameles sp. cf. *P. bougainville*		e.g. F18898, coll. Anderson and Clutton, 1926.
F. Thylacomyidae		
Macrotis lagotis		e.g. BM42663, BM43884, presented to BM in 1870 (see Krefft, 1870 who notes this species — as *Peraglea*, in Breccia Cave); F57917. O.C.
F. Phascolarctidae		
Phascolarctos sp.		No specimens available. Krefft (1870) notes *P. cinereus* from Breccia Cave.
F. Vombatidae		
Vombatus ursinus mitchellii	(T)	e.g. BM M10791, holotype, probably from Breccia Cave; MF721, O.C. "Cave 4"; F58707, O.C. "Cave 4"; F31055, coll. Anderson & Schevill, 1932. BC.
Lasiorhinus krefftii	(T)	e.g. BM 42601, holotype, coll. Krefft,1866 or 1869 in Breccia Cave.
Phascolonus gigas		e.g. MF728/9, transferred from Mining Museum, 1936.
Ramsayia magna		e.g. F5342, coll. by H. Barnes, 1885.
Genus indet. *medius*		e.g. UCMP 45148, coll. Marcus, 1954, Bone Cave. BC.

F. Diprotodontidae		
Subfam. Diprotodontinae		
Diprotodon optatum	(T)	e.g. BM M10796, holotype, coll. by Mitchell, 1830, in "the large cave". BC.
Diarcodon parvus	(T)	e.g. F50099, holotype, coll. J. Mahoney, 1954, in Bone Cave. This taxon is in need of revision.
Zygomaturus trilobus		e.g. UCMP LFM124, coll. in Bone Cave by Marcus, 1954.
Subfam. Palorchestinae		
Palorchestes azeal		e.g. MF452, transferred from Mining Museum, 1936; F7272, holotype *P. rephaim*, coll. Barnes (see Woods, 1958). BC.
Palorchestes parvus		e.g. F30646, F30645. O.C.
Palorchestes sp.		e.g. F31047, coll. Anderson & Schevill, 1932.
F. Petauridae		
Pseudocheirus sp.		e.g. BM M3651 (see Lydekker, 1887).
F. Phalangeridae		
Trichosurus sp. cf. *T. vulpecula*		e.g. F62091, F62092 coll. in Bone Cave by Hope, 1963, 1976. Noted in Breccia Cave by Krefft (1870). CC, BC.
F. Thylacoleonidae		
Thylacoleo carnifex		e.g. F51287, O.C., labelled "No. 4 Cave" = Cathedral Cave; F4664, coll. H. Barnes, "3 Cave" = Breccia Cave; F18666, coll. Anderson & Clutton, 1926. CC, BC.
F. Potoroidae		
Propleopus sp.		e.g. UCMP 45171, coll. in Bone Cave by Marcus, 1954.
Aepyprymnus rufescens		e.g. UCMP 45189, coll. in Breccia Cave, Marcus, 1954; F18899, coll. Anderson & Clutton, 1926. CC, BC.
Bettongia sp.		e.g. UCMP 57387, UCMP 57388, coll. Wellington Caves (general) by Marcus, 1954.
F. Macropodidae		
Subfam. Sthenurinae		
Sthenurus (Sthenurus) atlas	(T)	e.g. UCMP 45193, coll. Bone Cave, Marcus, 1954.
Sthenurus (Sthenurus) andersoni		e.g. UCMP 57373, UCMP 64967, coll. in Wellington Caves (general) by Marcus, 1954.
Sthenurus (Simosthenurus) oreas		e.g. F31026, coll. Anderson & Schevill, 1932, BC.
Sthenurus (Simosthenurus) orientalis	(T)	e.g. F10201, holotype. O.C.
Sthenurus (Simosthenurus) pales		e.g. F31041, coll. Anderson & Schevill, 1932.
Procoptodon rapha	(T)	e.g. F19652, holotype, coll. Krefft, 1869, Breccia Cave; UCMP 57385, coll. Bone Cave by Marcus, 1954.
Procoptodon pusio		e.g. F19654, O.C.; Krefft (1870) notes several specimens of *Halmaturus thomsonii* (= *P. pusio*) from Breccia Cave.
Troposodon minor		e.g. F31012, coll. Anderson & Schevill, 1932; UCMP 45149, UCMP 45192, coll. in Bone Cave by Marcus, 1954. CC, BC.
Troposodon kentii		e.g. F31027, coll. Anderson & Schevill, 1932.
Subfam. Macropodinae		
Bohra paulae	(T)	e.g. AM F62099, O.C., no precise location data; referred tibia, F62101 from "4 Cave", collected by Ramsay, 1881.
Protemnodon brehus	(T)	e.g. F43303a, BM 43853, syntypes, coll. Krefft, 1866, 1869 in Breccia Cave; UCMP 54031, coll. in Phosphate Mine by Marcus, 1954. CC, BC.
Protemnodon anak		e.g. F18904/9, coll. Anderson & Clutton, 1926. BC.
Protemnodon sp. cf. *P. devisi*		Unregistered specimens BS.
Thylogale sp.		e.g. MF 304, transferred from Mining Museum, 1935.
Wallabia sp. nov.		Unregistered specimens. BS.
Macropus sp. cf. *M. giganteus*		e.g. MF 124, transferred from Mining Museum, 1934.
Macropus giganteus titan	(T)	e.g. BM M10777, holotype, from "Large Cavern", coll. by Mitchell, 1830; F18665, coll. Anderson & Clutton, 1926 in Phosphate Mine; UCMP 45164, coll. in Breccia Cave, Marcus, 1954. CC, BC.
Macropus robustus altus	(T)	e.g. UCMP 45155, coll. in Bone Cave by Marcus, 1954; F31029, coll. by Anderson & Schevill, 1943. BC.
Macropus wellingtonensis n.sp.	(T)	e.g. F31037, coll. Anderson & Scheville, 1932. BC.
Macropus agilis siva		e.g. UCMP 45174, coll. in Breccia Cave, Marcus, 1954. BC.
Macropus rankeni n. sp.	(T)	e.g. F31015, coll. Anderson & Schevill, 1932. BC.
Macropus sp. cf. *M. dryas*		e.g. F47077e, transferred from Mining Museum, 1964.

Macropus sp. cf. *M. rama*	e.g. F47115, transferred from Mining Museum, 1964.
Macropus sp. I	e.g. MF65, transferred Mining Museum, 1930. BC.
Macropus sp. II	e.g. F31041, coll. Anderson & Schevill, 1932. BC.
Petrogale sp. cf. *P. penicillata*	e.g. F47033, transferred from Mining Museum, 1964. BC.
Onychogalea sp. cf. *O. fraenata*	e.g. F31048, coll. Anderson & Schevill, 1932.
Largochestes leporides	e.g. F31044, coll. Anderson & Schevill, 1932. BC.
Genus indet. 1	e.g. MF47, MF63, transferred from Mining Museum, 1930; F30331, F30555. O.C.
Genus indet. 2	e.g. unregistered specimens. BC.

Note: New species mentioned in this list have been described by Dawson (1982), an unpublished Ph.D thesis.

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Some Pacific Criconematina (Nematata)

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ABSTRACT. Several new or little known Criconematina are reported from Fiji, New Guinea, Tonga and Western Samoa. *Paratylenchus tui* n.sp. from Vava'u, a northern island in the Tonga group, most resembles *P. vandenbrandei* De Grisse, 1962, in measurements and lateral field but the anterior portion of the head is modified into a prominent disc, offset by constriction, distinguishing *P. tui* n.sp. from this and other species. *Gracilacus aonli* (Misra & Edward, 1971) is redescribed from a Western Samoan population. A new genus, *Syro,* is described in the subfamily Criconematinae for four species (three of them new) indigenous to New Guinea and three known species from tropical Africa. The genus is based on criteria which have not formerly been much considered in the group or have been overlooked, namely: form of head, uneven arrangement of appendages around body, appendages (whatever their shape) produced by basic dichotomy at least posteriorly, and a short, triangular postvulval region of few annules bearing long dichotomous trailing appendages. The genus consists of: *S. vexillatrix* n.sp., *S. chrisbarnardi* (Heyns, 1970) n. comb., *S. coronatus* (Schuurmans, Stekhoven & Teunissen, 1938) n. comb., *S. dracomontanus* (Van den Berg, 1983) n. comb., *S. hughdavidi* n.sp., *S. orphreyifer* n.sp. and *S. melanesicus* (Andrássy, 1979) n. comb.; information additional to the original description is given on the last of these.

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KEYWORDS: plant nematodes, taxonomy, Criconematina, Pacific islands, New Guinea, Africa.

Several genera have been established to accomodate unusual species of Criconematina from Australia, New Zealand and the islands of the Central and South Pacific (*Blandicephalanema* Mehta & Raski, 1971; *Pateracephalanema* Mehta & Raski, 1971; *Colbranium* Andrassy, 1979 and *Amphisbaenema* Orton Williams, 1982). Considering the vastness of the region, the evolution within it of so many unique plants and animals and the scant attention it has received from nematologists, it would be surprising if there were not others. Among the taxa reported here is a group of closely related new species from New Guinea. These have clear affinities with three previously described species from Africa which have not hitherto fitted very satisfactorily into any of the existing genera. With the addition of one further species recently described from New Britain, all these are considered to constitute a new and distinct genus.

Materials and Methods

Species from New Guinea were recovered in a survey for plant parasitic nematodes undertaken by Drs John Bridge and Sam Page, Oct. – Dec., 1982; material from Fiji, Western Samoa and Tonga came from a survey which I made in the region during 1976 – 1977. Specimens were heat killed, fixed in either 4% formalin or F.A. 4:10, cleared in lactophenol and processed to glycerin containing traces of picric acid by a modified Baker method.

Abbreviations used in the tables are fully explained in Orton Williams, 1982. They include: L ex (distance of excretory pore from anterior end of body), L t (tail length), W1 ca (width of first cephalic annule, W1 ba (width of first body annule) and W v (width at vulva).

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Paratylenchus tui n.sp.

Fig. 1, A–L

Type material. The holotype female, nineteen female and three male paratypes are deposited at the Commonwealth Institute of Parasitology, St. Albans, Hertfordshire, England. Paratypes have been sent to the following institutions: Australian Museum, Sydney, New South Wales, Australia (four females); Agricultural University, Wageningen, The Netherlands (three females); University of California Nematode Collection, Davis, California, U.S.A. (three females) and United States Department of Agriculture Nematode collection, Beltsville, Maryland, U.S.A. (two females).

Type host and locality. Soil around the roots of the small indigenous tree *Alphitonia zizyphoides* (Spreng.) A. Gray, (Rhamnales), besides coast road one mile south-west of Tefisi village, island of Vava'u, Tonga. Collected 8/12/1976.

Description. FEMALES. Body ranging from eyebrow shaped, through hook shaped to an open spiral, thin to only slightly swollen in prevulval region. Annules fine anteriorly, often obscure, becoming larger and more distinct by base of conus, measuring 1.0–1.5 μm at midbody. Lateral field narrow with three incisures, the central line much less clearly marked than the outer pair. In transverse section (Fig. 1,I) the lateral field appears as a small pad of body cuticle with a shallow open V at centre.

Lip region truncate, modified into a flattened disc not resolvable into separate submedian lobes, between 3 and 4 μm across, expanded equally around the head, rounded at the edge and set off from rest of head by a posterior constriction. Immediate oral area projecting very slightly from centre of head disc. Cephalic sclerotization moderately developed, vestible rounded in outline. Stylet fine, flexible, conus 25–30 μm long. Stylet knobs angular, about 2.5–3.0 μm across, with small but definite outwardly directed points. Dorsal oesophageal gland orifice 4 or 5 μm from stylet base. Excretory pore immediately anterior to hemizonid or impaling it, sited between nerve ring and top of basal bulb. Hemizonid about two body annules long causing a slight bulge in the cuticle.

Ovary outstretched; spermatheca ovoid, averaging 8 x 10 μm, prominent in the majority of paratypes but in some a mass of sperm was present in the uterus and a separate spermatheca could not be distinguished. Cuticle anterior and posterior to vulva smooth for about two annule widths, especially in slender females. Vulval flaps well developed, rounded or flattened, with a well defined crenation at either end near the junction of flap and body cuticle. Postvulval region 40–60 (52) μm long with distinct annulation. Tail very variable 2–3.6 (2.6) anal body widths long, broadly or finely rounded to acute (Fig. 1, D–H).

MALES. More slender than females, an open C shape. Annulation not visible on head and neck, becoming more distinct further back, 0.7–1.2 μm at midbody. Lateral field with two definite incisures and possibly a central third one. Stylet absent, oesophagus degenerate, its boundaries obscure. Excretory pore at base of nerve ring. Spicules weakly cephalate, almost straight. Anal sheath moderately developed, measuring about 1.0–1.5 μm. Tail concave ventrally, convex dorsally, terminating in a short spike in all three specimens.

Differential diagnosis. The flattened head disc distinguishes *P. tui* n.sp. from the majority of *Paratylenchus* species but some degree of modification is also found in the labial region of *P. vandenbrandei* De Grisse, 1962; *P. coronatus* Colbran, 1965; *P. tateae* Wu & Townshend, 1973 and *P. labiosus* Anderson & Kimpinski, 1977. *Paratylenchus vandenbrandei* has roughly similar measurements and three lateral lines but a less pronounced lip region with a truncate anterior surface and a sharply conoid head contour joining the body at an angle. Annulation of the head is distinct. In *P. tui* n.sp. the head is not differentiated from the body posterior to the expanded labial disc, joins the body without an angle and is indistinctly annulated. Because of similarities in measurements and lateral field between the two species, these differences were checked on paratypes of *P. vandenbrandei* (slide R200 in the collection of Laboratorium voor Dierkunde, Rijksuniversiteit, Ghent, Belgium). *Paratylenchus coronatus* has a much less disc-like anterior than the new species, and one more line in its lateral field. Both *P.tateae* and *P. labiosus* have four lines in the lateral field and shorter stylet lengths (between 15 and 17 μm).

Etymology: *Tui,* the Tongan word for chief or king, is treated as an indeclinable noun and alludes to the crowned appearance of the head.

	Females		Males
	Paratypes	Holotype	Paratypes
n	30		3
L (μm)	215–280 (250)	252	220–235 (228)
St (μm)	33–40 (35.6)	39	–
a	16–27 (22.5)	20.2	25–29 (26.9)
b	2.8–3.7 (3.3)	3.1	–
c	12.9–22.2 (17.1)	15.8	17–19 (18.5)
V	77–82 (79.3)	79.4	–
L ex (μm)	54–66 (58.6)	63	51–53 (52)
L oes (μm)	72–85 (76)	81	–
Lt (μm)	12–22 (15)	16	12–13 (12.3)
Spicules, chord (μm)	–	–	14–15 (14.2)
Gubernaculum (μm)	–	–	2–3

Table 1. Morphometrics of *Paratylenchus tui* n.sp.

Gracilacus aonli (Misra & Edward, 1971) Raski, 1976

Fig. 2, A–K

Paratylenchus aonli Misra & Edward, 1971: 345, fig. 1.
Gracilacus aonli (Misra & Edward, 1971) Raski, 1976: 98

Remarks. When Raski (1976) revised *Gracilacus* he was unable to get access to the types of this species and based his account of it on the published description. This lacks some useful information whilst the accompanying illustrations are not as precise as they might be. Nevertheless, the specimens described here, from the roots of *Cerbera odollam* Geartn. on Upolu, the main island of Western Samoa, conform remarkably well to the measurements (Table 2), description and drawings given by Misra & Edward. A critical character in the identification was the presence of an elongate ovoid spermatheca. The spermatheca of *G. aonli* is

Fig. 1. *Paratylenchus tui* n. sp: **A**, habitus, both sexes. **B–I**, female: **B**, entire; **C**, anterior end; **D–H**, posterior ends; **I**, cross section midbody. **J–L**, male: **J**, anterior end; **K, L**, posterior ends.

described as 'oval, just above the uterus, about 9.5 μm across'; unfortunately its length was not given. In one of the illustrations however (Fig. 1G), an attenuated oval shape, not separated into spermatheca and uterus, strongly indicates the presence of an elongate spermatheca rather than one of about the same length as width. Such a spermatheca is found in comparatively few species (which are discussed below) and the appearance of this character in both *G. aonli* and the Western Samoan population increases the likelihood that they are conspecific.

Morphometrics. See Table 2.

Description. FEMALES. Body hook-shaped to an open spiral, sometimes slightly swollen in the immediate prevulval region. Annulation visible on head and neck, coarsening down body; midbody annules 1.1–1.7 μm. Lateral field of four incisures, the outer pair more distinct than the inner pair. Head weakly conoid, flattened anteriorly, the outer margins of the anterior surface slightly thickened suggesting the presence of minute submedian lobes; oral disc convex. Vestible rounded in outline, housing stylet tip, more strongly sclerotized than cephalic framework. Stylet fine, flexible, conus 50–56 μm long. Stylet knobs rounded, 2.5–3.5 μm across; dorsal oesophageal gland orifice about 5 or 6 μm behind stylet knobs. Hemizonid just anterior to excretory pore or impaled by it, sited at base of median bulb to nerve ring.

Spermatheca prominent, sausage shaped, rounded at the ends, 6–8 μm across by 20–30 μm long, 2.8–3.8 times longer than wide (exceptionally, in a single specimen 4.8 times), generally filled with sperm. Empty spermathecae appear thin walled but are still easily seen. Body scarcely constricted at vulva; postvulval region 58–72 (64) μm long. Vulval flaps present; small, rounded, not prominent. Tail coarsely annulated, 3.0–3.8 (3.5) anal body widths long; terminus variable, usually acute but sometimes finely to broadly rounded.

MALES. body C-shaped with distinct annulation throughout, including head, neck and tail. Lateral field with four incisures. Head shape resembling that of female. Stylet absent; oesophagus degenerate, its boundaries obscure. Spicules strongly cephalate, distal quarter bent at an angle. Anal sheath moderately developed (about 1.5 μm long). Tail often drawn out to acute terminus (Fig. 2, I) but not infrequently rounded (Fig. 2, J & K).

Differential diagnosis. *Gracilacus aonli* is characterized by four lines in the lateral field, a weakly conoid - truncate head and an elongate spermatheca which is at least two and a half times longer than wide. This last feature is shared in the genus only by *G. pandata* Raski, 1976, perhaps *G. goodeyi* (Oostenbrink, 1953) Raski, 1962 and *G. janai* Baqri, 1979. In the original description of *G. goodeyi* the spermatheca was said to be round and was illustrated as such but in a number of populations identified as this species by Geraert (1965), the spermatheca was of an elongate type. This point was not resolved by Raski (1976) when he revised *Gracilacus,* as the types available to him were in a useless condition. However, Oostenbrink, Geraert and Raski are in agreement that *G. goodeyi* has a strongly conoid head which tapers sharply to a narrow, rounded apex, a shape not likely to be confused with the weakly conoid truncate head of *G. aonli.*

Gracilacus aonli and *G.pandata* are morphologically very similar and can be distinguished only by the generally larger dimensions of the latter, particularly the total body length of both sexes. In *G. janai* the spermatheca is clearly illustrated as elongate but no mention of this (nor of its dimensions) is made in the text. The species can be differentiated from *G. aonli* mainly by its two lateral lines and absence of vulval flaps.

One further species with an elongate spermatheca is *G. raskii* Phukan & Sanwal, 1979, although here it is described as about twice as long as wide. Dimensions and head shape in this species closely resemble *G. aonli* and, from the description the main distinguishing features are this difference in length of spermatheca and lack of vulval flaps in *G. raskii.*

In addition to the Western Samoan population described here, I have also identified *G. aonli* from the roots of taro, *Colocasia esculenta* (L.) Schott, on Viti Levu, Fiji.

	Females		Males	
	Western Samoa	*Type Population	Western Samoa	*Type Population
n	13	25	7	15
L (μm)	255–305 (272)	250–310	240–285 (266)	280–340
St (μm)	59–66 (61)	55–65	–	–
a	21–25 (22.8)	9–26	22–28 (25.0)	24–34
b	2.4–2.8 (2.5)	2.5–3.0	–	3–4.5
c	11.2–14.2 (12.5)	14–20	11–14 (12.1)	10–14
V	75–78 (76.4)	76–84	–	–
L ex (μm)	77–88 (82)	75–90	62–73 (68)	65–70
L oes (μm)	103–112 (106)	–	–	–
Lt (μm)	18–25 (22)	–	20–25 (22)	–
Spicules (μm)	–	–	16–18 (17)	16–18
Gubernaculum (μm)	–	–	3–3.5 (3.1)	3.5–4.4

*From Misra & Edward, 1971

Table 2. Morphometrics of *Gracilacus aonli* Misra & Edward, 1971

Nothocriconema polynesianum Orton Williams, 1982. Fig.2, L–N

Nothocriconema polynesianum Orton Williams, 1982: 245, Figs 4 & 5.

Remarks. One population of females from a mixed vegetable planting at Talipiko, Southern Highlands, New Guinea was studied. Specimens closely resembled the types from Western Samoa and Tonga but were longer, had longer stylets, a higher annule number and generally greater dimensions (see Table 3), annular margins were rough, often looking frayed, although they could not be called crenate. Additionally, most

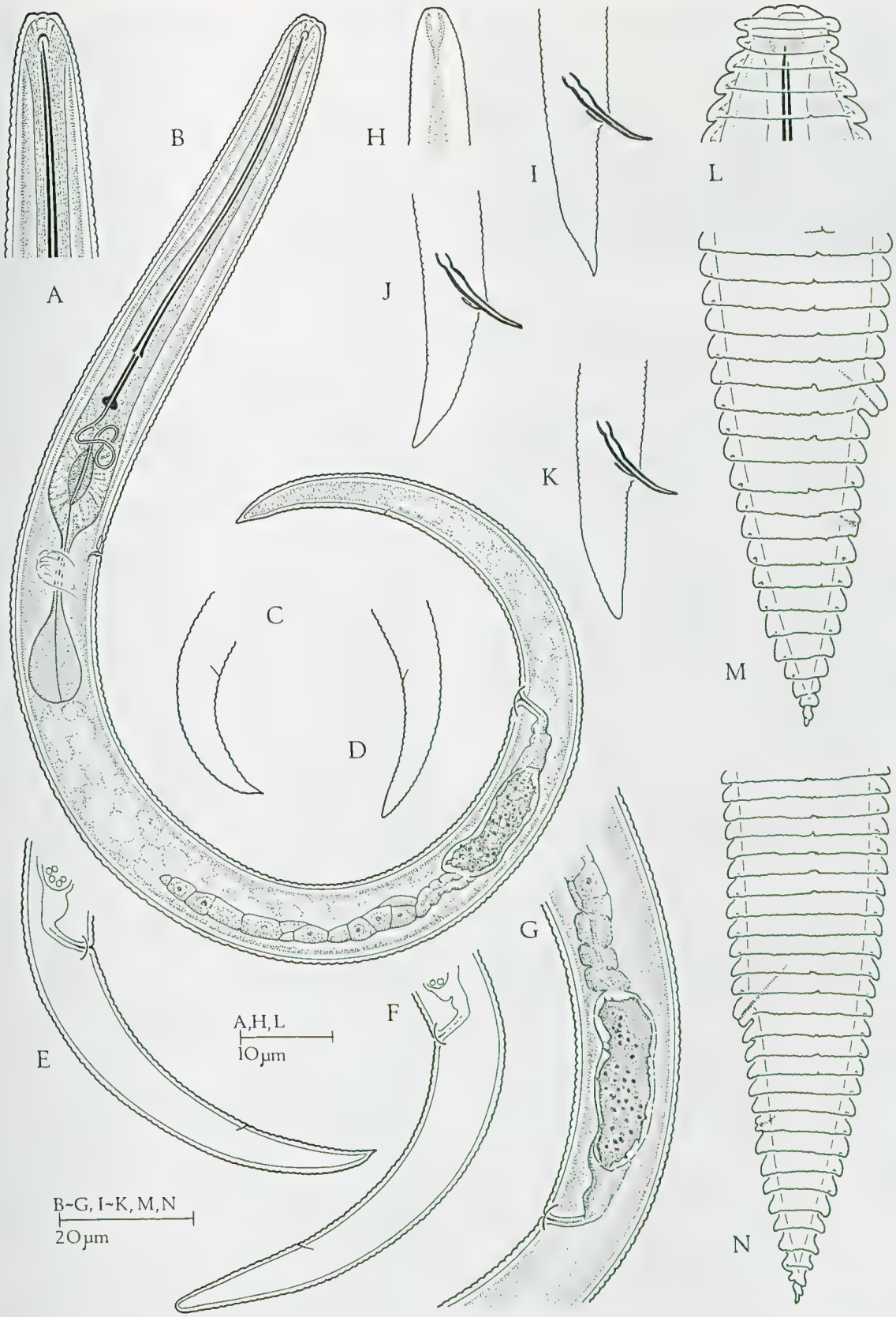

Fig. 2. A–K, *Gracilacus aonli* (Misra & Edward, 1971) Raski, 1976. **A–G,** female: **A,** anterior end; **B,** entire; **C–F,** posterior ends; **G,** region of spermatheca. **H–K,** male: **H,** anterior end; **I–K,** posterior ends. **L–N,** *Nothocriconema polynesianum* Orton Williams, 1982: **L,** female, anterior end; **M, N,** female, posterior ends.

specimens had a small notch, indentation or other irregularity in a midlateral position on some body annules particularly between midbody and anus. Re-examination of holotype and paratypes of *N. polynesianum* showed that this feature is present in the type series also although not as pronounced as shown in Fig. 2, M & N. This gives another diagnostic character to the species and puts it closer to *N. acriculum* Raski & Pinochet, 1976, from which it can be differentiated by its wider first head annule than second (in *N. acriculum* the first head annule is narrower than the second) and less drawn out tail.

	Females		
	Western Samoa* (Type population)	Tonga*	New Guinea
n	32	8	10
L (μm)	256-323 (290)	232-306 (281)	270-345 (320)
St (μm)	46-54 (50)	45-50 (47.6)	51-58 (55)
R	76-86 (82)	75-82 (78)	91-101 (95)
R sr	15-18 (17)	14-17 (15)	16-21 (19)
E oes	21-25 (23)	20-25 (22)	24-29 (26)
R ex	24-28 (26)	23-26 (25)	28-31 (29)
R v	11-15 (13)	12-14 (13)	15-19 (17)
R an	6-10 (8)	7-9 (8)	10-12 (11)
R van	3-6 (4)	3-4 (3.4)	4-7 (5)
L oes (μm)	65-80 (74)	65-77 (71)	75-87 (84)
L ex (μm)	74-96 (84)	71-92 (83)	80-102 (94)
L v (μm)	35-52 (42)	37-44 (49)	42-58 (48)
Lt (μm)	17-30 (22)	14-26 (20)	26-31 (28)
W1 ca (μm)	109-12 (11.2)	10.5-12 (11.2)	11-12.6(12)
W2 ca (μm)	9-11.5(10.7)	9.5-11.8 (10.5)	10.5-12.5(11.5)
W1 ba (μm)	12.5-15 (14)	12.8-15.5(14)	12.5-16.5(14)
W v (μm)	20-25 (23)	22-26 (24)	21-27 (25)
a	8.4-11.7 (10.3)	9.6-11.4 (10.6)	10.3-11.6(10.9)
b	3.4-4.6 (3.9)	3.3-4.4 (3.9)	3.4-4.0 (3.8)
c	10.7-17.4(13.3)	11.9-18.4(14.5)	10.5-12.5(11.4)
V	83.9-89.3(85.7)	85.4-88.0(86.5)	83.1-85.9(85.0)

*From Orton Williams, 1982

Table 3. Morphometrics of *Nothocriconema polynesianum* Orton Williams, 1982.

Syro n. gen.

This genus is erected in the subfamily Criconematinae Taylor, 1936, for seven species, four indigenous to the Central and Western Pacific and three from Africa. The several criteria used in defining it have not previously been given much consideration in the group (e.g. head form) or have not been reported (i.e. dorsal and ventral halves of the animal morphologically different). By these and the other criteria used for the genus, the species have strong affinities although they do not resemble each other closely.

Type-species. *S. vexillatrix* n. sp.

Other species. *S. chrisbarnardi* (Heyns, 1970) n. comb.
Syn. *Criconema chrisbarnardi* Heyns, 1970
Crossonema chrisbarnardi (Heyns, 1970) Loof & De Grisse, 1973
Ogma chrisbarnardi (Heyns, 1970) Andrássy, 1979

S. coronatus (Schuurmans Stekhoven & Teunissen, 1938) n. comb.
Syn. *Ogma coronatum* Schuurmans Stekhoven & Teunissen, 1938
Criconema coronatum (Schuurmans Stekhoven & Teunissen, 1938) De Coninck, 1943
Crossonema coronatum (Schuurmans Stekhoven & Teunissen, 1938) Mehta & Raski, 1971
Seriespinula coronata (Schuurmans Stekhoven & Teunissen, 1938) Andrássy, 1979

S. dracomontanus (Van den Berg, 1983) n. comb.
Syn. *Crossonema dracomontanum* Van den Berg, 1983

S. hughdavidi n. sp.

S. melanesicus (Andrássy, 1979) n. comb.
Syn. *Seriespinula melanesica* Andrássy, 1979
Crossonema melanesicum (Andrássy, 1979) Ebsary, 1981

S. orphreyifer n. sp.

Diagnosis. FEMALES. Body fusiform, thick, rounded at both ends, of small to medium length (285–643 μm) with a low number of coarse annules (39–63). Head of one annule expanded anteriorly, posteriorly collar-like; pseudolips present, sublateral lobes absent. Body bearing numerous appendages; those on main portion arranged either in longitudinal rows or horizontally across annules but in either case, unequally distributed between dorsal and ventral halves and more concentrated dorsally. Main body appendages simple, bifurcate, or with several points, often dichotomizing. Posterior appendages greatly modified, elongate, sometimes 'antler-like', showing evidence of one or more dichotomies. Terminal appendages extending beyond posterior end of body, often profusely branched, dichotomizing. Stylet 57–103 μm. Vulva with strongly developed lips, conoid, projecting beyond level of adjacent annules. Postvulval region of 4–8 annules (generally 5 or 6), triangular in shape, wider than long (VL/VB = about 0.6).

JUVENILES. With 12–14 longitudinal rows of scales, each scale divided into two equal parts by a deep bifurcation, and bearing two or more terminal spines on each part (type-species).

MALES. Unknown.

Differential diagnosis. *Syro* has a number of similarities to *Crossonema* Mehta & Raski, 1971, as typified by *C. civellae*. The different head form of this species (of two annules as defined below, and lacking a pronounced collar), equal distribution of appendages around body and presence of alternating palmate appendages, not formed from successive dichotomy at the posterior end, render it distinct.

Etymology. *Syro*, from $\sigma\upsilon\rho\omega$ = I trail (something behind) treated as a masculine Latin noun.

Remarks. *Syro* is characterized by four main features:

1. The form of the head. In all species this is composed of a single annule with an expanded, outwardly directed anterior portion and a pronounced, collar-like posterior portion, often tapering towards the base. This is seen in each of the new species described here (Figs 3,A & B; 4,C; 5,B), and is illustrated by De Coninck (1945) for *S. coronatus* and Andrássy (1979) for *S. melanesicus*. I take the head to extend posteriorly to the base of the cephalic sclerotization only, and consider the second head annule mentioned by Andrássy and the second and third of De Coninck to be, in reality, body annules. In *S. hughdavidi* n. sp., the external form of the second annule is such that it might be connsidered either as a second head annule or as a first body annule. Using the extent of the labial sclerotization as a definition, it is part of the body, leaving the head with a single annule.

2. The unequal arrangement of appendages around the body. This was found by chance after sectioning a female of *S. vexillatrix* n. sp. (Fig. 3, D) and subsequently checked, as far as possible, on all the material. It is difficult to see on laterally mounted specimens and is unlikely to have been noticed on the single female from which *S. chrisbarnardi* was described (Heyns, 1970). Andrássy (1979) did not mention this feature in his description of *S. melanesicus* either, but there is a slight dorsal shift to the scale rows on a specimen of this species from Western Samoa which I examined. There are indications in De Coninck's illustrations of *S. coronatus* that some sort of difference between the dorsal and ventral halves of the body occurs in *S. coronatus;* the same is true in illustrations of *S. dracomontanus*, see Van den Berg (1983). The three species newly described here clearly demonstrate this difference which is most obvious in *S. orphreyifer*. One species outside *Syro, Seriespinula octozonale* (syn. *S. sokliense*), is also known to have scale rows unequally arranged around the body (see Momota & Ohshima, 1974; Choi & Geraert, 1975).

3. The presence of elongate, dichotomously branched appendages trailing posterior to the terminus. The terminal appendages of all species show this dichotomous form, and those of *S. orphreyifer* and *S. hughdavidi* paticularly can be seen to have attained their form by successive dichotomies. In these two species the appendages also dichotomize over most of the body.

4. Short triangular postvulval region (of greater width than length) with a strongly modified projecting vulva.

Syro vexillatrix n. sp.

Fig. 3, A–K

Type material. The holotype female, nine female and two juvenile paratypes are deposited at the Commonwealth Institute of Parasitology, St. Albans, Hertfordshire, England. A single female has been sent to each of the following institutions: Australian Museum, Sydney, New South Wales, Australia; Agricultural University, Wageningen, The Netherlands; University of California Nematode Collection, Davis, California, U.S.A. and United States Department of Agriculture Nematode Collection, Beltsville, Maryland, U.S.A.

Type host and locality. Soil from the rhizosphere of *Crotalaria lunata* Beddome ex Polhill (Sabaceae), a small shrub native to Southern India, at Tobua, Nembi Plateau, Southern Highlands, New Guinea. Collected 4/11/1982. Populations 2–4 were associated with sweet potato, *Ipomoea batatas* (L.) Lam. or vegetable garden soil at other localities in the Southern Highlands.

Morphometrics: See Table 4.

Description. FEMALES (all populations). Body stout, fusiform, slightly curved, heavily covered by detritus in all but a few specimens. Head of one annule, its anterior margin expanded, outwardly or partly forwardly directed and coarsely crenate. Lip region simple with pseudolips but lacking sublateral lobes. Remainder of head collar-like, tapering posteriorly, 13–15 μm across at base. Total height of head 7–8 μm.

Body annules retrorse, well separated from each other; first body annule wider than head. Annules bearing appendages arranged in longitudinal rows over much of the body, except anteriorly to about the level of the stylet base. In this region, appendages randomly spaced, neither absolutely in longitudinal rows nor alternating (Fig. 3, A & K). Appendages mostly simple, triangular, with finely rounded points but sometimes bifid. At stylet base, appendages forming up into 12–16 longitudinal rows unequally spaced around body (Fig. 3,D) and concentrated on the dorsal side. Appendages short (4–6 μm) midbody, generally bifurcate, although 1, 3 and 4 pronged forms were seen. Between appendages, annular margins appearing smooth, rough or, in one specimen, finely crenate (somewhat exaggerated in Fig. 3, F & G). Appendages of vulval region and posterior becoming increasingly elongate, branching dichotomously to form large flaps which often have two narrow, outwardly directed prongs, sometimes with a third, shorter, central prong, or, rarely, branch twice. Appendages reaching 28 μm in length at terminus, trailing behind the animal for up to 20 μm.

Stylet moderately developed, conus 78–88 μm long, knobs strongly pointed, of greater width than height, 11–14 μm across. Dorsal oesophageal gland orifice about 4 or 5 μm behind knobs. Gonad typical; spermatheca not seen. Vulval lips pronounced, extending beyond line of annules but not to level of appendage ends. Vulva closed, lips forming a chamber internally (Fig. 3,I & J). Postvulval length 10–26 μm, 0.3–0.7 of vulval body width; postvulval region sharply conoid, almost an equilateral triangle in optical section, with a broadly rounded terminus composed of several lobes, the bases of the terminal appendages. Anus not seen.

JUVENILES. Two were found. Appendages arranged in longitudinal rows, 12–14 in number but difficult to

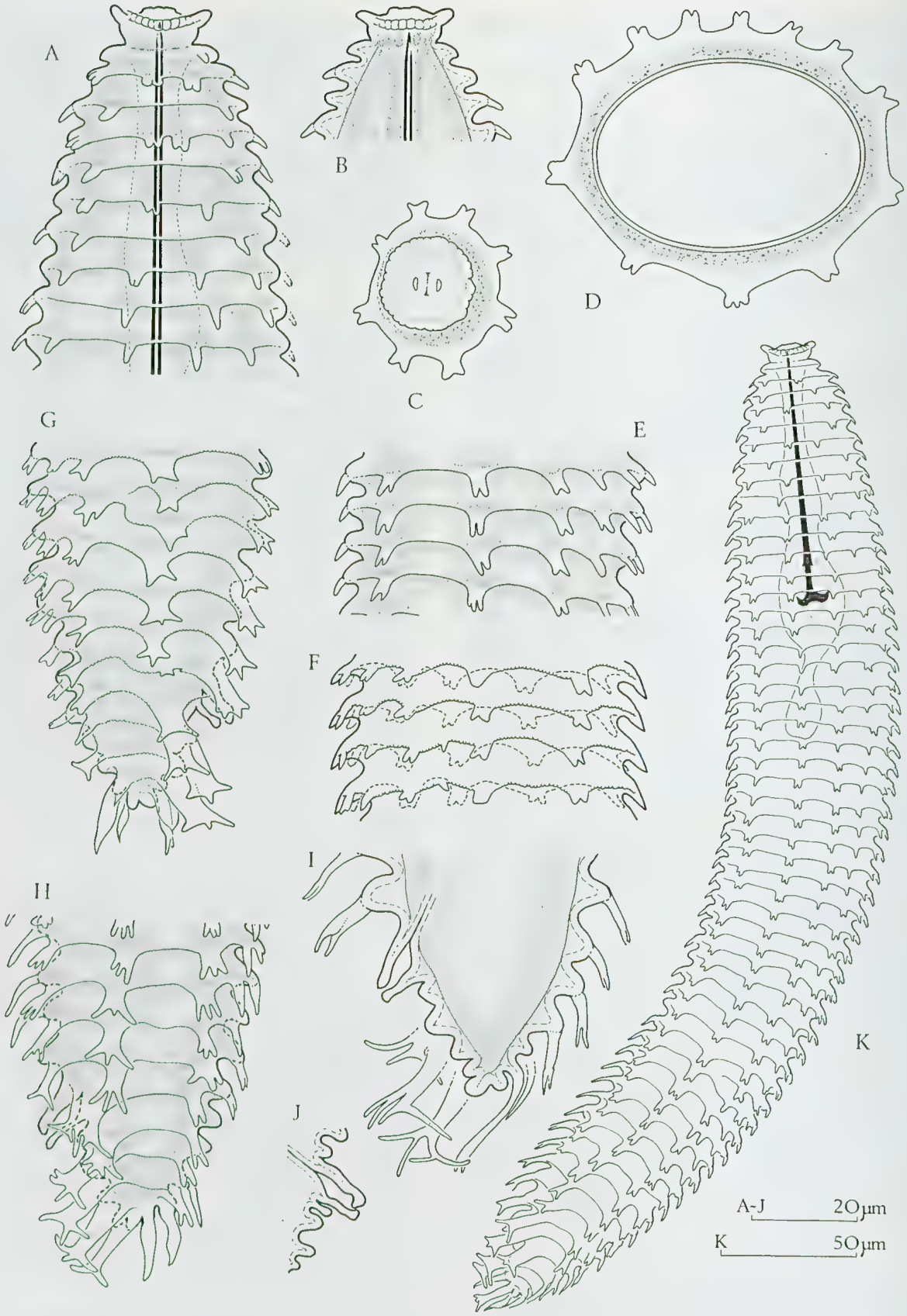

Fig. 3. *Syro vexillatrix* n. sp., female: **A, B**, anterior ends; **C**, face view; **D**, cross section midbody; **E, F**, annules midbody (dorsal side to the right in E, the left in F); **G–I**, posterior ends; **J**, vulval region; **K**, entire. **Note**: the rings of stippling in C and D indicate detritus.

count accurately. Appendages prominent, deeply divided into two equal parts by an inverted V-shaped bifurcation, the distal end of each part bearing two (sometimes more) fine spikes.

MALES. Not found.

Differential diagnosis. *Syro vexillatrix* n.sp. is most closely related to *S. coronatus* and *S. chrisbarnardi,* a subgroup of the genus, all with the appendages on the anterior quarter of the body differing from the main body appendages in arrangement or kind (or both) but with the terminal appendages very similar in type. *Syro vexillatrix* can be distinguished from *S. coronatus* by the triangular, widely separated scales of its anterior region (compared with the almost continuous line of squarish scales in this species) and the lack of ornament on the terminal appendages (which are clubbed, with minute papillae in *S. coronatus*). It more resembles *S. chrisbarnardi* in general morphology but has bifurcate appendages over most of the body instead of simple ones, and 12–16 scale rows instead of 8. Information about *S. coronatus* has been taken mainly from De Coninck (1945) who redescribed the type specimens, in preference to the original description of Schuurmans Stekhoven & Teunissen (1938) which contains a number of inaccuracies.

Etymology. *Vexillatrix,* a neo-Latin noun for a female standard bearer, in reference to the type-species and the banner-like appearance of some of the terminal appendages.

Females

	Type pop	Pop 2	Pop 3	Pop 4	Total range	holotype
n	3	5	3	1	12	
L (μm)	383–495	334–465	395–526	450	334–526 (431)	383
St (μm)	94–103	95–102	101–103	94	94–103 (99)	94
R	57–59	56–63	58–61	46	46–63 (58)	57
R st	14–15	14–18	15–17	11	11–18 (15)	14
R oes	19–20	17–23	19–22	15	15–23 (20)	19
R ex	–	19–20*	22*	–	20–22* (20)	–
R v	5–6	5–6	5–6	6	5–6 (6)	6
L oes (μm)	130–157	133–148*	126–148	139	126–157* (141)	133
Wl ca (μm)	18	19–21	19–21	20	18–21 (20)	18
Wl ba (μm)	22–24	21–25	23–25	25	22–25 (23)	22
a	6.0–8.1	6.1–8.2	6.8–8.9	7.1	6.0–8.9 (7.0)	6.4
b	2.9–3.2	2.5–3.3	2.9–3.8	3.2	2.5–3.8 (3.1)	2.9
V	94.5–96.0	94.7–97.0	96.2*	94.9	94.9–96.2 (95.5)	95.0

*not measurable in all specimens

Table 4. Morphometrics of *Syro vexillatrix* n.sp.

Syro orphreyifer n. sp.

Fig. 4, A–F

Type material. The holotype female is deposited at the Commonwealth Institute of Parasitology, St. Albans, Hertfordshire, England.

Type host and locality. Soil from the rhizosphere of sweet potato, *Ipomoea batatas* (L.) Lam. at Kuari Kogu, Tari, Southern Highlands, New Guinea. Collected 1/11/1982.

Description. HOLOTYPE FEMALE: L = 285 μm (excluding trailing appendages), 300 μm (including appendages); a = 5.3; b = 2.7; c = ?; V = 96.1; stylet = 74 μm (conus = 62 μm). Body almost straight, stout, fusiform, with 39 coarse annules dorsally and ventrally (including head and terminus), packed with detritus. Annules bearing elongate appendages, mostly bifurcate but sometimes trifurcate or more with rounded distal ends. Appendages borne in two distinct arragements which succed each other on alternate annules down the length of the body. First arrangement: appendages completely encircling the body, continuous along the posterior margin of the annule, numbering about 60 on midbody annules; those borne dorsally 5–7 μm long, gradually increasing in size around the body to those occupying a midventral position which are 9–11 μm long. Second arrangement: commencing on the fourth annule behind head, appendages forming a semicircle around the dorsal half of the body only, all about 5–7 μm long, except those at the very ends of the semicircle which are midlateral in position and slightly smaller. The ventral half of such annules is devoid of appendages. From about the 12th annule from terminus, both sets of appendages becoming more elongate and branched. Terminal appendages up to 27 μm long, extending about 15 μm beyond terminal cuticle, profusely branched. All appendages with two or more prongs have divided in a basically dichotomous manner.

Head of one annule, anteriorly much expanded and saucer shaped, 20 μm across with a strongly crenate margin; posteriorly, a broad tapering collar, 11 μm across at base. Oral disc prominent; sublateral lobes absent. Total height of head 7.5 μm. Stylet occupying 11 annules, knobs 9.5 μm across. Dorsal oesophageal gland orifice not visible. Oesophagus 105 μm long; isthmus very short, 25 μm behind stylet base. Excretory pore not seen.

Gonad typical; spermatheca present, oval 11x17 μm, filled with sperm. Vulva sited on the fourth annule from terminus between two ventrally scaleless annules, projecting beyond them, conical, closed. Postvulval region conoid, triangular, about 11 μm long (to base of terminal appendages), 0.5 times vulval body width. Terminus a confused mass of appendage bases.

JUVENILES. Not found.

MALES. Not found, although the sperm in the spermatheca of the holotype female indicates that they exist.

Differential diagnosis. The alternating arrangement of appendages that completely encircle the body, or are confined to its dorsal half on successive body annules, is unique to *S. orphreyifer* and immediately differentiates it from all known criconematids.

Etymology. From *orphrey,* a late Middle English word for a richly decorated band on a garment, + *ifer* = a Latin suffix denoting carrying.

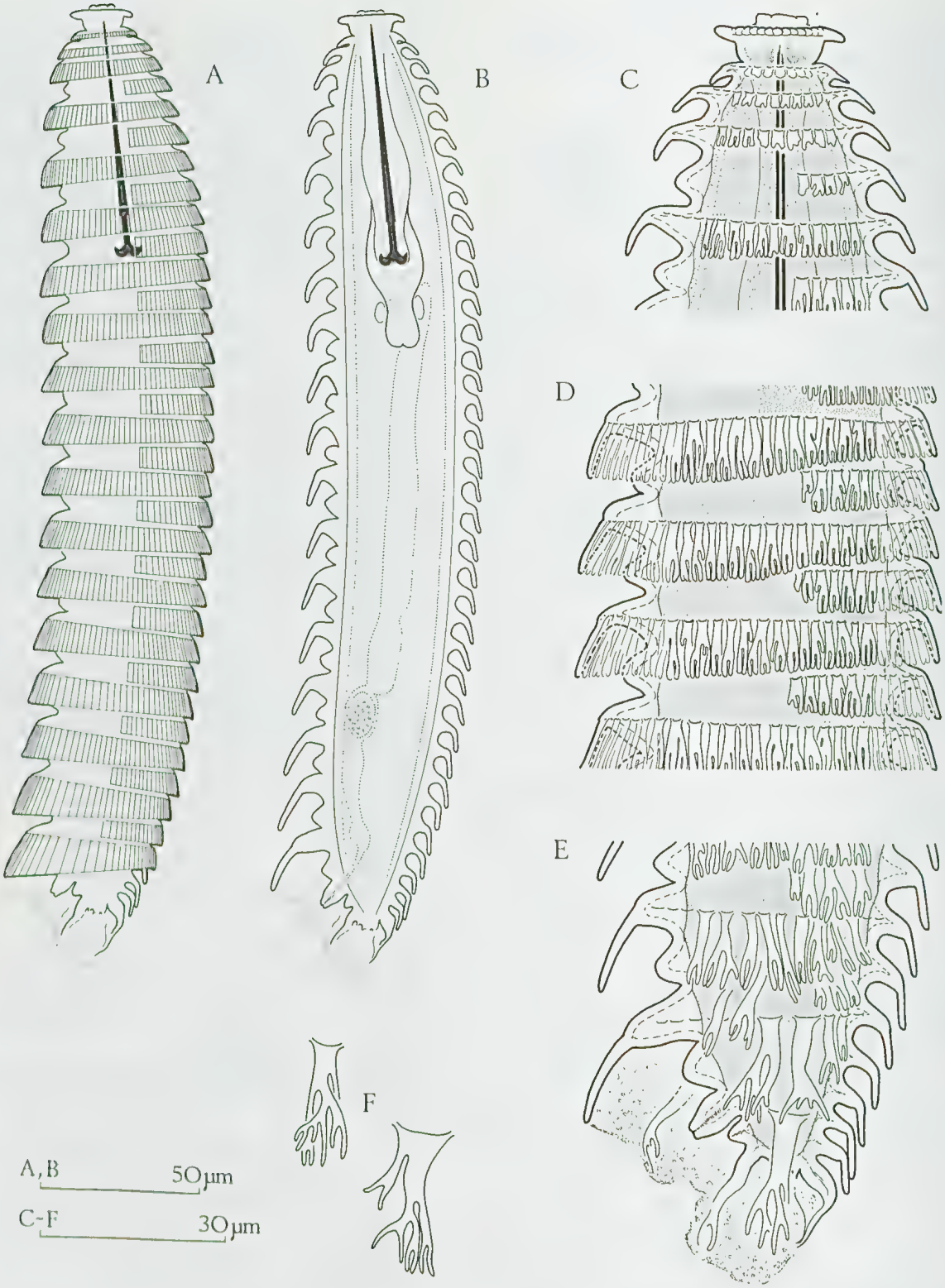

Fig. 4. *Syro orphreyifer* n. sp., female: **A**, entire, surface view; **B**, entire, optical section; **C**, anterior end; **D**, annules midbody; **E**, posterior end; **F**, terminal appendages. **Note**: detritus indicated at terminus only; dorsal side to the right in all except **F**.

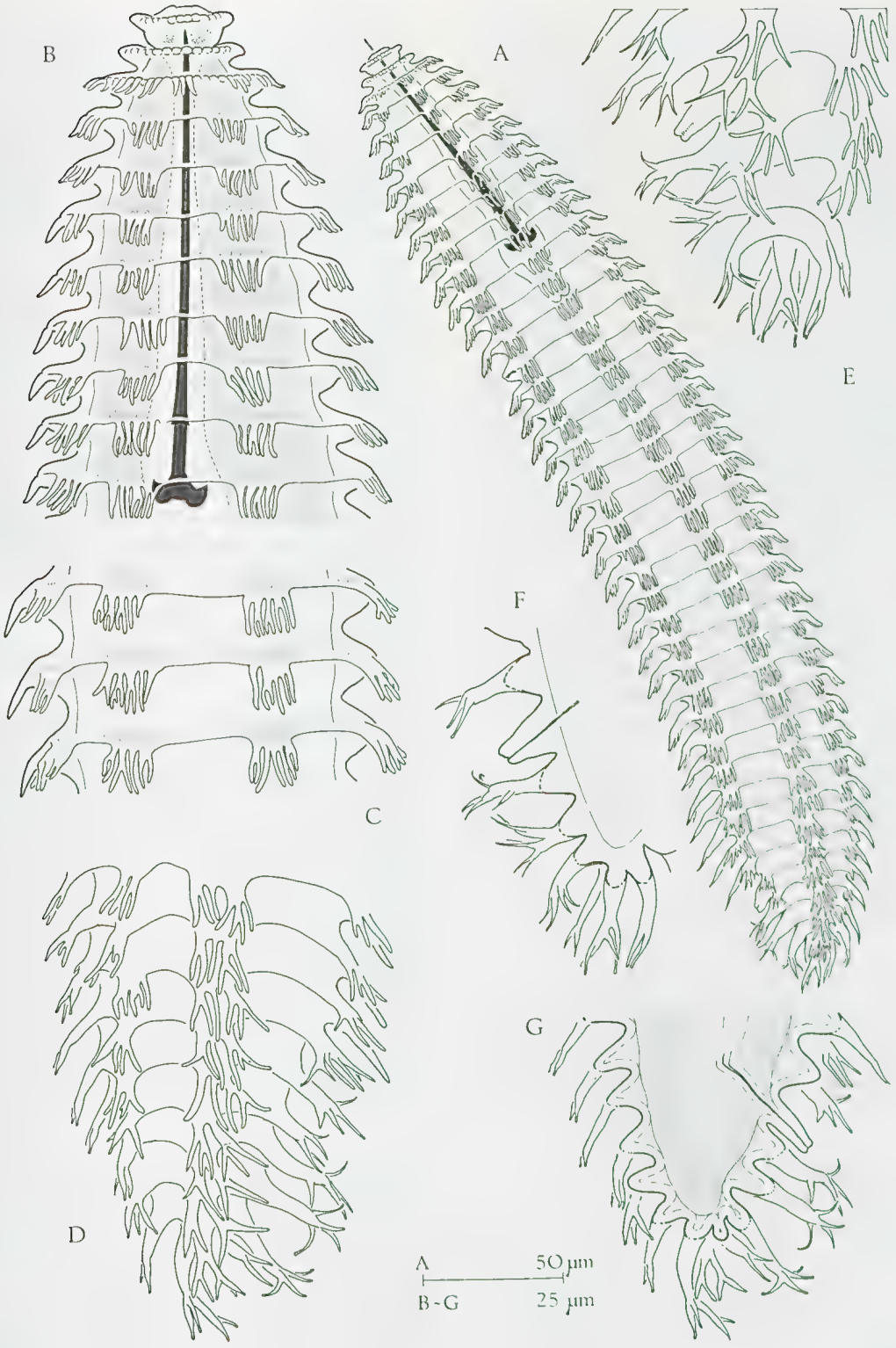

Fig. 5. *Syro hughdavidi* n. sp., female: **A**, entire; **B**, anterior end; **C**, annules midbody; **D–G**, posterior ends. **Note:** in B–D the dorsal side is to the left.

Syro melanesicus (Andrássy, 1979) n. comb.

Seriespinula melanesica Andrássy, 1979: 41, fig. 9
Crossonema melanesicum (Andrássy, 1970) Ebsary, 1981: 106

Remarks. This unusual and readily identified species was based on two females from rain forest in New Britain. A single female which came from the roots of taro, *Colocasia esculenta* (L.) Schott, Savai'i island, Western Samoa, was seen in this study. Although rather flattened on mounting, the following can be given: L = 295 μm, stylet = 68 μm (conus = 54 μm), R = 51, Rv = 6.

Compared with the types, the samoan specimen has a slightly shorter stylet and lower number of both of body annules and postvulval annules. However, the most obvious differrence is that only eight rows of palmate appendages are present, not the ten rows of Andrássy's population. These could be counted clearly on the flattened specimen. Compared with the other species of *Syro,* the scale rows are not much shifted to the dorsal side of the body but the difference remains detectable.

Syro melanesicus has strong affinities with one other species, that is *S. hughdavidi* n. sp. which is described below. Body appendages of *S. melanesicus* do not dichotomize and are very much as illustrated by Andrássy. One or two of the terminal appendages appear to be formed from tubular outgrowths of the cuticle at the margin of the annule, and branch distally in a dichotomous manner similar to *S. hughdavidi*, but ventrally, in the vulval region, appendages remain palmate and unbranched, and it would be difficult to confuse the two species.

Syro hughdavidi **n. sp.**

Fig. 5, A–G

Type material. The holotype female and single female paratype are both deposited at the Commonwealth Institute of Parasitology, St. Albans, Hertfordshire, England.

Type host and locality. Soil from the rhizosphere of sweet potato, *Ipomoea batatas* (L.) Lam. at Usa village, Kagua, Southern Highlands, New Guinea. Collected 29/10/1983.

Description. FEMALES. Holotype female: L = 545μm (including posterior appendages), a = 7.5, b = 4.1, c = ?, V = 92.3%, stylet = 98 μm (conus = 82 μm), R = 44. Paratype female: L = 382 μm (including posterior appendages), a = 5.2, b = 3.3, c = ?, V = 90.0, stylet = 91 μm (conus = 77 μm), R = 41.

Body fusiform , stout, rounded at both ends. Head of one annule, expanded anteriorly, 18–19 μm across, its margin outwardly directed and distinctly crenate; posteriorly tapering as a slightly convex collar, 12 μm across at base. Total height of head 6.5 μm.

Appendages arranged in 10 longitudinal rows over most of the body, slightly shifted dorsally so that there appear to be 4 rows on the ventral half and 6 on the dorsal. Appendages compound, composed of single digitate spines and bifurcate spines, together forming groups of 5–9 projections with distally rounded ends. Appendages becoming condiderably elongate posteriorly and dividing more than once to form 'antler-like' processes (Fig. 5,D). From vulval region to terminus some appendages are formed from tubular extensions of the body cuticle extending from the body almost at right angles and branching dichotomously, becoming needle-like distally. These fine spikes sometimes have a small terminal swelling. Posterior appendages up to 17 μm in length.

Stylet strongly developed, extending over 11 annules; basal knobs 10–11 μm across. Excretory pore opening on 15th or 16th annule, appendages lacking in its immediate vicinity. Gonad typical, with small ovoid spermatheca filled with sperm. Vulva on 5th annule from terminus with well developed lips extending beyond line of adjacent annules but not to level of surrounding appendages. Body width at vulva 47–52 μm, twice the vulva – terminus length of 24–25 μm (measured to base of terminal appendages). Anus not seen. In optical section (Fig. 5,G), terminus broadly rounded with several lobes which form the bases of the terminal appendages.

JUVENILES. Not found.

MALES. Not found, although the sperm in the spermatheca of the holotype female indicates that they exist.

Differential diagnosis. *Syro hughdavidi* n. sp. most resembles *S. melanesicus* (both have ten longitudinal rows of several-pronged appendages) but the ornamentation of the body is more exaggerated. The palmate groups of processes are commonly bifid, become elongate posteriorly and branch dichotomously several times. Tubular extensions of the body cuticle terminating in needle-like spikes are also present in profusion. Additionally, *S. hughdavidi* has a differently shaped head, greater stylet length (91–98 μm compared to 68–71 μm) and fewer body annules (41–44 compared to 51–60).

Etymology. The species is named in memory of my brother Hugh David.

ACKNOWLEDGEMENTS. I thank Dr A. De Grisse, Rijksuniversiteit, Ghent, Belgium for the loan of types of *Paratylenchus vandenbrandei;* staff of the Royal Botanic Gardens, Sydney, Australia for verifying the name of *Crotalaria lunata,* and the Director and staff of the Commonwealth Institute of Parasitology, St. Albans, England for laboratory space, facilities and many kindnesses during my visit in 1983. I am most grateful to Dr John Bridge (C.I.P.) for permitting me to study and describe the criconematid material collected in New Guinea.

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Paramisophria variabilis, a New Arietellid (Copepoda: Calanoida) from Hypersaline Waters of Shark Bay, Western Australia

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Abstract. Both sexes of *Paramisophria variabilis* n. sp. (Copepoda: Arietellidae) taken in plankton samples from hypersaline (50.00–56.5 ‰) waters of Shark Bay, Western Australia, are described. A key to differentiate the known species of the genus is presented,

McKinnon, A. David & William J. Kimmerer, 1985. *Paramisophria variabilis*, a new arietellid (Copepoda: Calanoida) from hypersaline waters of Shark Bay, Western Australia. Records of the Australian Museum. 37(2):85–89.

Keywords: Copepoda, Arietellidae, *Paramisophria*, taxonomy, Western Australia, hypersaline waters.

The genus *Paramisophria* comprises three species, the type *Paramisophria cluthae* T. Scott, 1897, *P. spooneri* Krishnaswamy, 1959 and *P. ammophila* Fosshagen, 1968. *Paramisophria cluthae* is known from Scotland (T. Scott, 1897) and Norway (Sars, 1903, Matthews, 1967, Fosshagen, 1968). Fosshagen (1968) commented that Tanaka's (1966) record of *P. cluthae* from Japan may represent the first record of another species. *Paramisophria spooneri* was described from bottom fauna collections off Plymouth, U.K. (Krishnaswamy, 1959), and *P. ammophila* from shallow water collections in the northeastern Bahamas (Fosshagen, 1968).

This paper describes a fourth member of the genus, taken in plankton samples on the Fauré Sill, a region of high tidal flow on the seaward side of Hamelin Pool, the southernmost region of the eastern gulf of Shark Bay, Western Australia. We sampled repeatedly using a 150 μm plankton net suspended 2.0 m under the anchored boat for periods of 30 minutes, over an entire tidal cycle. Once obtained, samples were stained with neutral red for 1 hour, then fixed in 10% formalin. Salinities ranged from 50.0‰–56.5 ‰.

We mounted specimens on microslides in polyvinyl lactophenol, and drew them using a Wild M20 phase contrast microscope and camera lucida. Further examination was made with an Olympus microscope with Nomarski optics.

Family Arietellidae Sars, 1902

Genus *Paramisophria* T. Scott, 1897

Type-species: *Paramisophria cluthae* T. Scott, 1897

The genus was established by T. Scott (1897) based on females only. Sars (1902) presented a description of both sexes of *P. cluthae* and a complete generic diagnosis. Fosshagen (1968) made several additional comments on the morphology of *P. cluthae*. Krishnaswamy (1959) altered the generic diagnosis to accommodate an endopod on the fifth leg of the male.

Key to Species of *Paramisophria*.

1. Exopod of antenna 2-segmented.....2

——Exopod of antenna with more than 2 segments.....3

2. Segments of antenna with 0, 4 setae respectively. Inner margin of female leg 5 coxa bifid, male (? right) leg 5 with a 1-segmented endopod extending from coxa to distal margin of 2nd exopod segment.....*P. spooneri*

——Segments of antenna with 4, 4 setae respectively. Inner marginal projection of female leg 5 coxa a distinct small spine. Males unknown...*P. cluthae* (sensu Tanaka)

3. Exopod of antenna 3- or-4-segmented. Male leg 5 with an endopod.....4

——Exopod of antenna 6-segmented. Inner marginal projection of female leg 5 coxa a distinct small spine. Male leg 5 with no endopod.....*P. cluthae*

4. Exopod of antenna 3-segmented. Inner marginal projection of female leg 5 coxa a sharp point continuous with the segment. Male leg 5 with a 1-segmented endopod on left leg, about equal in length to half the outer margin of the first exopodite segment.....*P. variabilis*

——Exopod of antenna 4-segmented. Inner marginal projection of female leg 5 coxa a distinct small spine. Male leg with a 1-segmented endopod on left leg, about equal in length to the outer margin of the first exopodite segment .....*P. ammophila*

Paramisophria variabilis n. sp.

Figs 1–2.

Material examined. Fifteen adult females, 17 adult males and 25 copepodids collected in plankton, Fauré Sill channel, Shark Bay, Western Australia (25° 58' S, 114° 03' E) between 2230 on 16 Jun. 1983 and 0630 on 17 Jun. 1983 by W.J. Kimmerer.

Type-material. Holotype female (Reg. No. P34778), allotype male (Reg. No. P34779) and 4 paratypes (Reg. No. P34780) of each sex deposited in the Australian Museum. The holotype, allotype, 2 paratype females (Reg. Nos. P34781, P34782) and 3 paratype males (Reg. Nos. P34783, P34784, P34785) dissected and mounted on microslides. An additional 2 paratypes of each sex deposited in Museum of Victoria (Reg. No. J3141) and Western Australian Museum (Reg. No. WAM44-84).

Description. FEMALE: body length, to end of furcal rami 1.64 mm. Prosome (Fig. 1a, b) robust and ovoid in dorsal view, and deep in lateral view. Posterodorsal margins of 2nd and 3rd pedigers each produced into 2 lobes, symmetrical about the mid-line. Posterior margin of prosome produced into a sharp dorsal projection on each side.

Rostrum (Fig. 1c) with 2 subequal, ventrally-directed filaments. Antennule 21-segmented, resembling that of type-species. Antenna (Fig. 1d) biramous, with 2-segmented basipod. Exopod 3-segmented; proximal segment bearing 3 setae on the distal margin; short middle segment bearing 1 seta; 3rd segment bearing 1 seta at about midpoint and 2 setae terminally. Terminal region of 3rd segment with a fold in the integument just proximal to insertion of terminal setae, giving impression of 4th segment. Endopod 2-segmented; proximal segment bearing a short lateral seta at about 80% of its length; distal segment with group of 3 setae at about 50% of its length, a short subterminal seta, and terminal group of 5 setae.

Mandible blade (Fig. 1e,f) of 4 large teeth, the outermost the largest and separated from other 3; 2 patches of denticles proximal to group of 3 teeth. Palp (Fig. 1e) 4-segmented; 2nd segment bearing 2 setae on outer distal margin; 3rd segment bearing flat projection carrying a single seta; 4th segment with 1 marginal and 4 terminal setae.

Maxillule (Fig. 1g) with 4 thick spines on proximal endite, and a stout trinagular denticle at their base (Fig. 1h); endopod with 2 terminal setae; exopod with 3 terminal setae.

The maxilla, maxilliped and first 4 swimming legs resembling those of type-species. Swimming legs armature formula (outer margin first; Roman numerals spines, Arabic numerals setae):

Leg 1	coxa 0–1	basis 1–1	exopod I–1; I–1; II–I–4
			endopod 0–1; 0–2; 1–2–2.
Leg 2	coxa 0–1	basis 0–0	exopod I–1; I–1; III–I–5
			endopod 0–1; 0–2; 2–2–4
Leg 3	coxa 0–1	basis 0–0	exopod I–1; I–1; III–1–5
			endopod 0–1; 0–2; 2–2–4
Leg 4	coxa 0–0	basis 1–0	exopod I–1; I–1; III–I–5
			endopod 0–1; 0–2; 2–2–3

Leg 5 (Fig. 2b,c,d) uniramous, 3-segmented; inner distal margin of basis produced into a sharp point, just proximal to which is a large plumose seta; setae of each side slightly asymmetrical. Segment 3 (exopodite) bearing 3 stout outer spines, distal of which is smaller, plus 2 terminal spines, separated by a thorn, outermost larger.

MALE: Body length, to end of furcal rami, 1.42 mm. Form of body resembling female, but urosome 5-segmented (fig. 1i). Antennules 21-segmented, left with weakly geniculate terminal segment (Fig. 1j). Antennae, mouthparts and swimming legs resembling those of female.

Right 5th leg 5-segmented (Fig. 2e,i); 2nd segment (basis) bearing an outer seta; 3rd segment bearing an outer marginal spine; 4th segment with a spine on outer margin at about 60% of its length. Inner margin of 4th segment produced into a broad lamella, at distal margin of which is a patch of fine hairs. Terminal segment bearing 3 finger-like projections.

Left leg 5 (Fig. 2e,f) with an outer seta on the 2nd segment (basis) and bearing a 1-segmented vestigal endopod, different in shape in all animals examined (Figs 2e,f,g,h). Segment 3 with an outer distal spine;

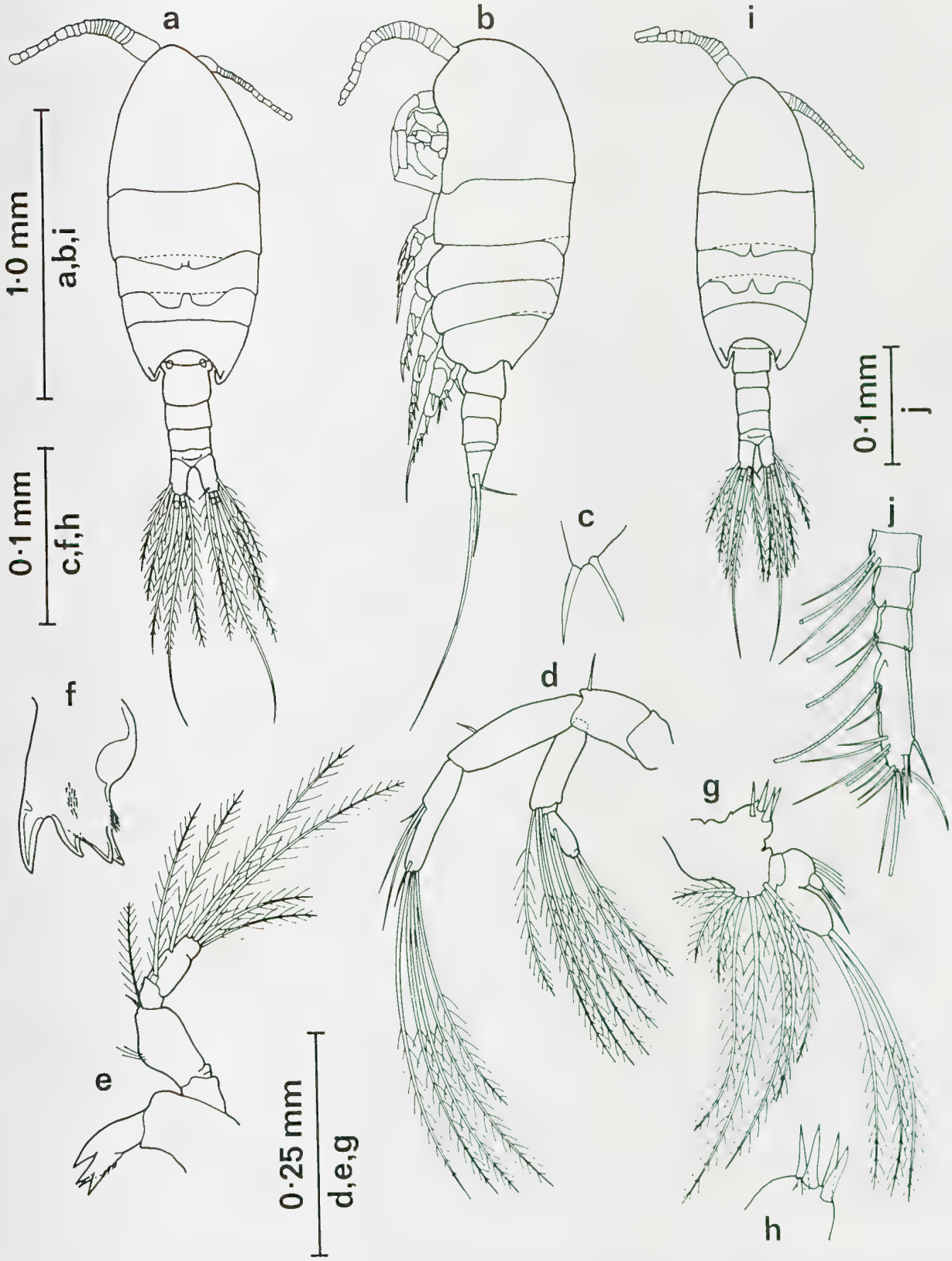

Fig. 1. Holotype female (a) dorsal, (b) lateral, (c) rostrum, (d) antenna, (e) mandible, (f) mandible blade, (g) maxillule, (h) proximal endite of maxillule. Allotype male (i) dorsal, (j) segments 15–18 of left antennule.

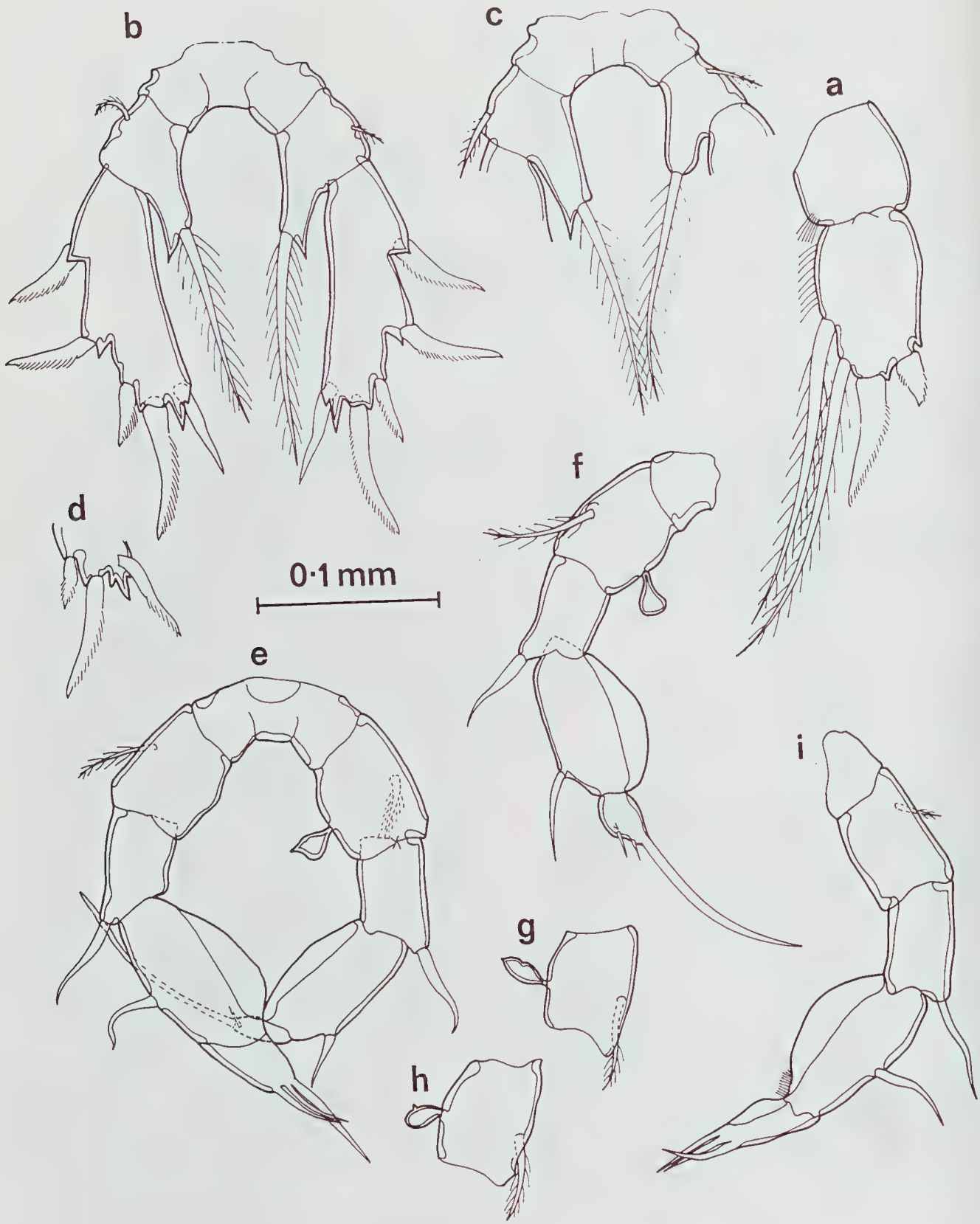

Fig. 2. (a) Abnormal leg 2 exopodite, paratype female (Reg. No. P34782); (b) leg 5, holotype female; (c) basal segments of leg 5, paratype female (Reg. No. P34782); (d) distal margin of right leg 5, paratype female (Reg. No. P34781); (e) leg 5, allotype male; (f) right leg 5 paratype male (Reg. No. P34785); (g), (h) basis and endopods of male paratypes (Reg. Nos P34784, P34783 respectively); (i) right leg 5 paratype male (Reg. No. P34785).

4th segment with an outer spine at about 75% length, produced on inner margin into a broad lamella. Terminal segment with a long, terminal spine-like projection, accounting for about 75% of its length, and 2 small spines on outer margin just proximal to base of projection.

Remarks. *Paramisophria variabilis* is named for the variability observed in its morphology, particularly in the endopod of the male leg 5. In addition, one female paratype (Reg. No. P34782) has an abnormal 2-segmented exopod on the 2nd leg (Fig. 2a) and asymmetrical coxae on leg 5 (Fig. 2c), the left of which is not produced into a sharp tip on the inner expansion of the coxa. Another female paratype (Reg. No. P34781) has an extra terminal thorn on the right exopodite of leg 5 (Fig. 2d).

Species of *Paramisophria* are similar in habitus, and the females are difficult to separate. The form of the male fifth leg provides the most distinctive feature. Dr A. Fosshagen (Blomsterdalen, Norway) is presently describing further species, one of which, from Midway Island, closely resembles *P. variabilis*. The male fifth leg of *P. variabilis* is most similar to *P. ammophila*, of the species described to date.

All species of *Paramisophria* are epibenthic. The Shark Bay material was collected in the plankton only because of the high turbulence in the area; the samples contained a lot of sediment and benthic animals. *Paramisophria variabilis* was not taken in any of the other 23 stations sampled along a transect from the Indian Ocean to Hamelin Pool (Kimmerer *et al.* in press). The present high salinity record implies considerable euryhalinity, however no salinity data is available for the other members of the genus.

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New Information on the Head and Shoulder Girdle of *Canowindra grossi* Thomson, from the Late Devonian Mandagery Sandstone, New South Wales

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ABSTRACT. The head of *Canowindra grossi* is redescribed from newly prepared casts of the holotype. The cheek has a fractionated postorbital series consisting of one large and two small postorbital bones; the lachrymal is small relative to the postorbitals and jugal, and the jugal is elongate. The opercular is deep, and higher than long. The skull table features a parietal shield without differentiated intertemporal, supratemporal or parietal bones. *Canowindra* shares with osteolepids plus eusthenopterids (Osteolepiformes) a large, externally ornamented anocleithrum, and a cheek with bar-like, vertical preopercular and single, large squamosal bone. It differs from these groups in the structure of the postorbital series and skull roof table. *Canowindra* represents an endemic genus which should be regarded as the only member of a taxon equivalent to osteolepids plus eusthenopterids. An amended diagnosis of the genus is given.

JOHN LONG, 1985. New information on the head and shoulder girdle of *Canowindra grossi* Thomson, from the Late Devonian Mandagery Sandstone, New South Wales. Records of the Australian Museum 37(2):91–99.

KEYWORDS: Osteichthyes, Osteolepiformes, Devonian, Australia, description, relationships, Porolepiformes, systematics.

Canowindra (Thomson, 1973) was the first crossopterygian genus known only from Australia. Prior to that work only fragmentary bones and scales of *Strepsodus decipiens* (Woodward, 1906) were documented from this country, and that identification has been questioned recently (Long, 1982). *Canowindra* is known from a complete natural mould in a slab of Mandagery Sandstone (Australian Museum F47153) collected in 1956 from a road cutting near the township of Canowindra. Besides the crossopterygian, the slab contains over a hundred well preserved armours of the antiarchs *Bothriolepis* and *Remigolepis*, and a partial armour of the euarthrodire *Groenlandaspis* (Dr A. Ritchie, pers. comm.). A Fammennian age is indicated by correlation with nearby marine intercalations containing brachipod faunas, and also by the abundance of the placoderm *Remigolepis* (Young, 1974; Long, 1983).

The new observations reported here resulted from further preparation of the original natural mould by Dr A. Ritchie and Mr R.K. Jones of the Australian Museum. The new latex cast of the head region reveals important features which could not be described by Thomson, and these are of great importance in discussing the phylogenetic position of the genus. Terminology used herein follows Jarvik (1980).

Description

The head is preserved in dorsal view with the cheeks, opercular bones and part of the pectoral girdle articulated (Figs 1, 2). Overall, the head is broad posteriorly and rather shallow with an acutely pointed snout. Sutures are not distinct on the fronto-ethmoidal shield but can be made out on the parietal shield and cheek. Laterosensory lines are not visible on any part of the head except for obscure pit-lines on the parietals, frontals, squamosals and dentary. Proportions of cranial bones are summarized in Table 1.

Fronto-ethmoidal shield. The fronto-ethmoidal shield reveals little new information. The presence of a large median postrostral (Thomson, 1973: 212) cannot be confirmed. Cracks on the surface suggest a polygonal bone mosaic at the front of the snout, although these do not appear as distinct sutures like the median line separating the frontals (Fr). A pineal foramen (Pin) appears to be present in the posterior

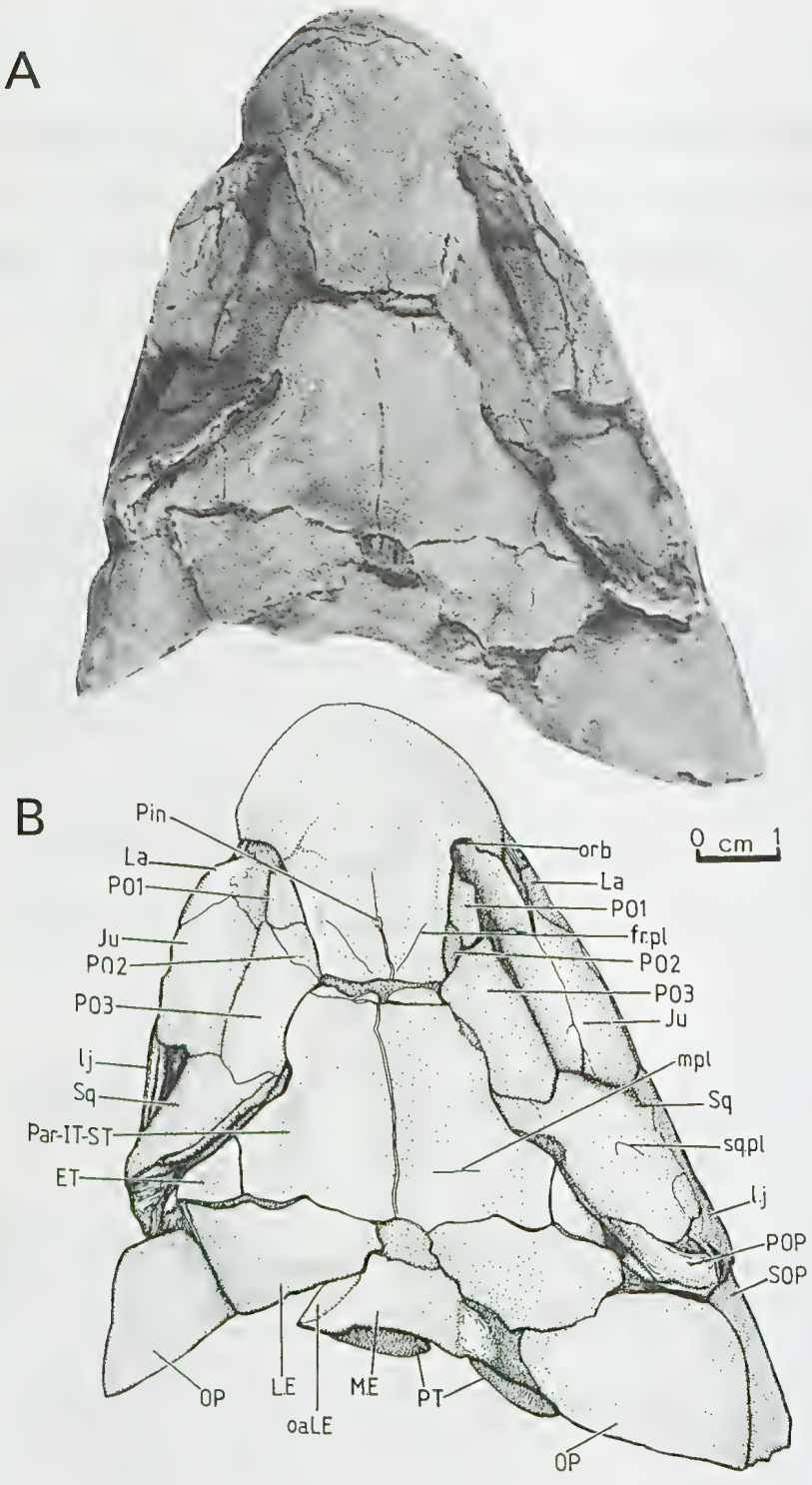

Fig. 1 *Canowindra grossi* Thomson: head of the holotype, Australian Museum F47153, in dorsal view. **A**, photograph; **B**, sketch interpretation. Abbreviations used in all figures: **AC1**, anocleithrum; **ac.pr**, anocleithral process; **Clth**, cleithrum; **ET**, extratemporal; **f.ex**, fenestra exonarina; **fr.pl**, frontal pit-line; **Ju**, jugal; **La**, lachrymal; **L.E**, lateral extrascapular; **l.j**, lower jaw; **Max**, maxilla; **M.E**, median extrascapular; **mpl**, middle pit-line of parietal; **oa.Cl**, area overlapped by cleithrum; **oa.LE**, area of median extrascapular overlapped by lateral extrascapulars; **oa.Pt**, area overlapped by post-temporal; **OP**, opercular; **orb**, orbit; **Par-IT-ST**, parieto-intertemporal-supratemporal; **Pin**, pineal foramen; **PO1, 2, 3**, postorbital bones; **PS**, prespiracular; **PSM**, preoperculosubmandibular; **POP**, preopercular; **PT**, post-temporal; **QJ**, quadratojugal; **SC1**, supracleithrum; **SOP**, subopercular; **Sq, Sq1, 2**, squamosal and accessory squamosals; **sq.pl**, squamosal pit-line.

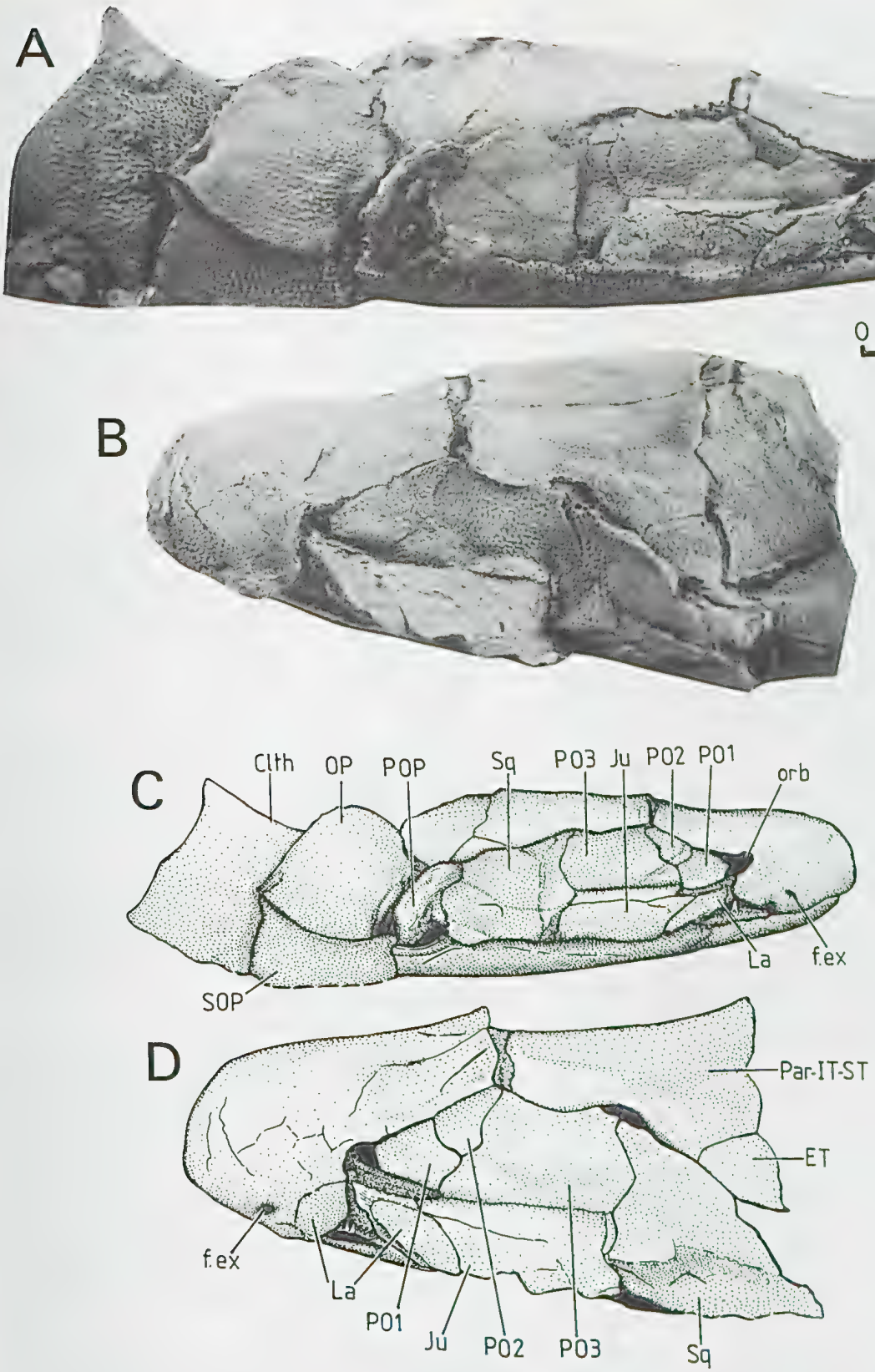

Fig. 2. *Canowindra grossi* Thomson. Interpretation of cheek bones of **A, C**, left side; and **B, D**, right side of holotype, Australian Mueum F47153. Abbreviations as for Fig. 1.

1. Length of fronto-ethmoidal shield	40 mm
2. Breadth of fronto-ethmoidal shield	36.5 mm
3. Diameter of orbit (r)	4.5 mm
4. Length of parietal shield	32.5 mm
5. Breadth of parietal shield	60 mm
6. Length of lateral extrascapular (l)	17.5 mm
7. Breadth of lateral extrascapular (l)	27 mm
8. Median length of median extrascapular	10.5 mm
9. Breadth of median extrascapular	27 mm
10. Length of cheek (r)	74 mm
11. Height of cheek (r)	25 mm
12. Length of postorbital 1	11.5 mm
13. Length of postorbital 2	11 mm
14. Length of postorbital 3	25.5 mm
15. Length of jugal	36 mm
16. Length of squamosal	32 mm
17. Greatest depth of opercular	33 mm
18. Greatest breadth of opercular	22 mm

Table 1. Cranial measurements of *Canowindra grossi*

third of the shield. Faint lines parallel to the lateral edges of the postorbital region of the shield could be sutures for the dermosphenotics. The frontal pit-lines (fr.pl) are clearly seen, and run posteriorly almost to the rear of the shield. The fenestra exonarina (f.ex) is well defined on both sides as a narrow anteroventrally directed slit. Below each of the small orbits there is a crescentic suture marking the anterior extent of the lachrymal (La).

Parietal shield. As Thomson (1973: 212) observed there are no sutures between the parietal, intertemporal and supratemporal bones of each side, though clear sutures separate the extratemporal bones (ET) from the rest of the shield, and a median suture separates the parietals. Fused parietals and intertemporal bones are known in porolepiforms and actinistians (Andrews, 1973), but fused parietal-intertemporal-supratemporals are unique to *Canowindra*. Unlike osteolepids, which may not show the sutures between these bones because of a cosmine cover (Jarvik, 1948), *Canowindra* has no cosmine. The parietal shield is notably broad, with a breadth/length index of 194. The width of the straight anterior margin is 32% of the posterior margin width. The posterior margin has two distinct notches on each side, one at the suture with the extratemporal bone and the other about midway between this and the midline. Posterior processes are present along the posterior margin at the mesial corners of the lateral extrascapulars, leaving a concave area for the short articulation area of the median extrascapular. The extratemporal bones are slightly narrower than Thomson's figure (1973, Fig. 2) suggests. They are still broader than long and contact the lateral extrascapular for 40% of the breadth of that bone.

Extrascapulars. The lateral extrascapulars (L.Ex) are extremely broad, being 44% as long as broad with irregularly notched anterior margins which contact the parietal shield. The median extrascapular (M.Ex) is also very broad, having a paramedian length one third of the total breadth. It is overlapped laterally by the lateral extrascapulars, as in osteolepiforms. The posterior margin has a strong median embayment.

Cheek. The bones of the cheek are clearly seen on the new cast. The postorbital of Thomson (1973, Fig. 3A) consists of two separate bones divided by a curved suture. As these two bones are present on both sides of the specimen, and laterosensory lines are not easily detected anywhere on the head, it is simpler to accept that this line is a suture dividing small postorbital bones, rather than the infraorbital sensory line canal, as implied by Thomson. The bone posterior to these two small anterior postorbitals occupies the area dorsal to the jugal and directly anterior to the squamosal, and is thus a postorbital bone rather than a prespiracular (Thomson, 1973, Fig 3A). The prespiracular bone occurs only in the cheeks of the porolepiform fishes, where it occupies a position posterior to the postorbital (which is immediately dorsal to the jugal), and dorsal to the squasmosal. It does not contact the jugal in *Porolepis* (Fig. 3C), *Glyptolepis*, *Holoptychius* or *Laccognathus* (Jarvik, 1972; Vorobyeva, 1980), and therefore is most probably a subdivision of the squamosal bone (Thomson, 1973: 219) which may be highly subdivided in some porolepiforms (e.g. *Holoptychius* Jarvik, 1972). In *Canowindra*, the area dorsal to the jugal, anterior to the single large squamosal and posterior to the orbit is therefore occupied by three postorbital bones, viz a large posterior element and two small anterior bones (Fig. 3B).

Each of the two small postorbital bones (PO1, PO2) is approximately half as long as the large subrectangular posterior postorbital. The anterior postorbital (PO1) is almost rhombic with a shorter posterior division, and contacts the other small postorbital at a concave suture. The posterior small postorbital (PO2) tapers posteriorly to an acute point at the junction of the fronto-ethmoidal and parietal shields. The large postorbital (PO3) has relatively straight dorsal and ventral margins, and the anterior margin slopes anteroventrally and is almost straight apart from a small median concavity. The posterior margin is strongly convex.

The jugal (Ju) is clearest on the right cheek, although on both sides the anterior end of the bone is missing. It is unusual in being a slender bone, three times longer than high. It is assumed to have formed the posterior margin of the orbit, as in other rhipidistians.

The lachrymal (La) is imperfectly preserved on both sides. It lies anterior to the jugal, which it meets along a curved suture, thus placing a large portion of the lachrymal ventral to the jugal. The lachrymal extends a short distance anterior to the orbit, and is bordered ventrally by the maxilla.

The squamosal (Sq) is the largest cheek bone, occupying 42% of the total cheek length. As in osteolepiforms it contacts the postorbital and jugal anteriorly, the maxilla and presumably the quadratojugal ventrally, and the preopercular

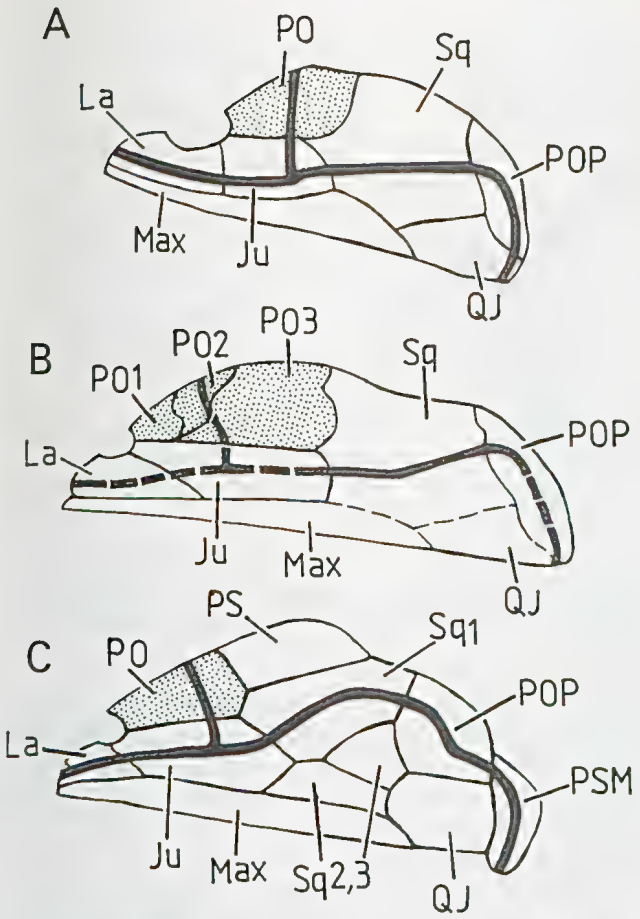

Fig. 3. Rhipidistian cheek bone patterns. **A**, Osteolepiformes (*Eusthenopteron*, after Jarvik, 1980); **B**, *Canowindra grossi*; **C** Porolepiformes (*Porolepis*, after Jarvik, 1972). Postorbital bone or series shaded; sensory-line canals represented by heavy lines. Abbreviations as for Fig. 1.

posteriorly. The anterior margin has two concavities for receiving the convex posterior borders of the jugal and postorbital bones. There is a cuspate squamosal pit-line (sq.pl) visible on the right side located close to a thin depressed line on the bone surface, the preopercular sensory line (pop). The squamosal is approximately two thirds as high as long.

The preopercular (POP) is clear on the right side, firmly attached to the posterior margin of the squamosal. It is a slender bone, three times as long as broad, with a vertical disposition, as in osteolepiforms (Fig. 3A, B).

Although the maxilla cannot be seen on the specimen, it is presumed to have been relatively slender, as Thomson has restored it (Thomson, 1973, Fig. 3A) in order to fit into the available space ventral to the lachrymal, jugal and squamosal bones. The short ventral extent of the preopercular supports this view.

Opercular bones. Only the operculars (OP) and the dorsal region of the subopercular (SOP) is preserved on the specimen. The opercular is much deeper than in Thomson's restoration (1973, Fig. 3A). It is almost one and a half times as deep as broad, extending ventrally from the lateral extrascapular along the complete posterior margin of the cheek. The posterior margin of the opercular is gently convex, the anterior margin relatively straight, and the ventral margin is distinctly convex.

The subopercular has a concave dorsal margin, not a convex one as restored by Thomson. It would appear from the relative position of the lower jaw that the subopercular was not a deep bone, but significantly longer than high.

Lower jaw. There is little new information to add to Thomson's comments. The dentary is slender posteriorly, broadening evenly towards the front, as in osteolepiforms. A posteriorly directed segment of the most posterior infradentary pit-line is present near the articulatory sockets of the mandible.

Pectoral girdle. Thomson (1973: 214) suggested that the cleithrum (Clth) was a double structure, composed of two separate ossifications. It is clear from the new cast that only the dorsal section of this bone is preserved on the right side, the ventral division being folded underneath the specimen. The ventral edge of this bone, as referred to by Thomson, is actually an irregular line caused by breakage of the cleithrum. The pectoral fin seen emerging from this area is partly obscured by the tail squamation of a nearby *Remigolepis*. The dorsal margin of the cleithrum is slightly concave, with a posterodorsal process. The posterior margin of this division of the cleithrum is quite concave.

There is an anocleithrum (ACl) on the left side of the specimen immediately posterior to the cleithrum. It resembles a large scale with a very extensive ventral overlap surface (oa.Cl) and an anteriorly directed anocleithral process (ac.pr; Fig. 4A). The ornamented region of the bone is approximately twice as large as that of the nearby scales, being much the same breadth.

The supracleithrum (Scl) is seen as a small, scale-like bone, anteromesial to the anocleithrum on the left side of the specimen (Fig. 4A). It is slightly larger than the nearby scales and has a broad dorsal overlap flange for the post-temporal bone (oa.PT). In life, only a small part of the supracleithrum was overlain by the opercular.

The post-temporals (PT) are identified as the two subrectangular bones posterior to each of the lateral extrascapulars. The post-temporal is of similar size to the supracleithrum, and contacted a large region of the posterior margin of the lateral extrascapular when articulated in the shoulder girdle (Fig. 4B).

Relationships of *Canowindra*

The unique plexus of characters exhibited by *Canowindra* is not typical of either osteolepiform or porolepiform fishes. Thomson suggested that it was closer to holoptychioids on skull and cheek structure (1973: 216, 217) but was not sure of its affinities. The

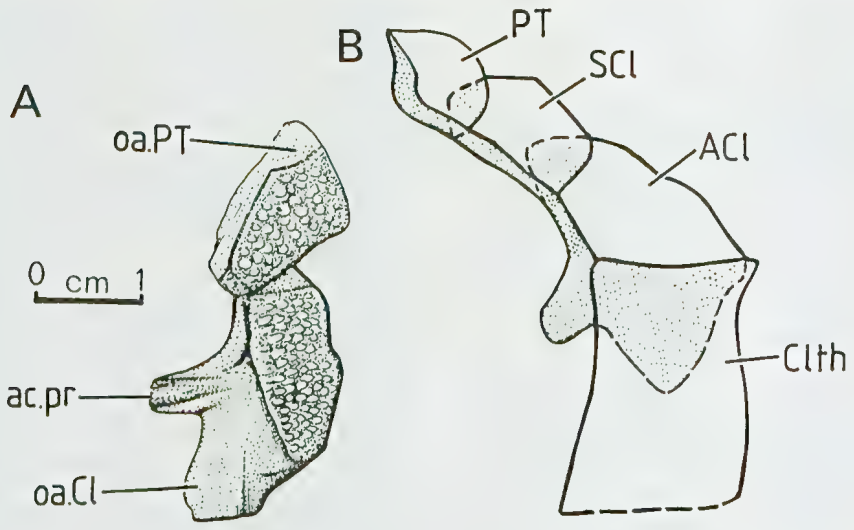

Fig. 4. *Canowindra grossi* Thomson. **A**, two of the dorsal pectoral girdle bones, the anocleithrum (below) and supracleithrum (above); from left side of holotype, Australian Mueum F47153. **B**, attempted reconstruction of the dorsal exoskeletal pectoral girdle bones of *Canowindra*. Overlap areas shaded.

porolepiform features of *Canowindra* are its broad parietal shield with large extratemporal bones and fused parietal-intertemporal bones, and the small orbits. Osteolepiform features of *Canowindra* are: cheek with a large single squamosal and vertical bar-like preopercular, the dermal shoulder girdle with a large, externally ornamented anocleithrum (Long, 1985), a single pair of external nares, median extrascapular overlapped by lateral extrascapulars, and a median boss on the basal surface of the scales. The loss of cosmine in the dermal skeleton and presence of rounded scales would further suggest that the genus is specialized, unlike the primitive members of both porolepiforms and osteolepiforms which bear rhombic scales and have an extensive cosmine cover (Jarvik, 1980). Unique features of *Canowindra* are the fusion of the parietal-intertemporal-supratemporal bones, the subdivision of the postorbital bone in the cheek, and the unusual shape of the median extrascapular.

Characters used to distinguish Osteolepiformes from Porolepiformes which are relevant to *Canowindra* are summarized in Table 2, taken from Jarvik (1972, 1980) and Long (1985). Despite recent suggestions that the osteolepiforms are a paraphyletic group (Rosen *et al.*, 1981), arguments for the monophyly of the group have been advanced (Long, 1985). From this list of characters it can be seen that *Canowindra* shares the following synapomorphies with Osteolepiformes: overall structure of the cheek, shoulder girdle with large anocleithrum. Characters of *Canowindra* in common with porolepiforms, such as the fusion of the intertemporal and parietal bones, and small orbits, can not be shown to be synapomorphies. Actinistia have a similar type of parietal shield to Porolepiformes (Andrews, 1973), and several groups of osteichthyans show that orbit size is a variable feature, such as in the primitive palaeoniscoids *Cheirolepis* and *Moythomasia* (Pearson, 1982), the osteolepiform *Glyptopomus* (Jarvik, 1950) and the dipnoans *Dipnorhynchus* and *Chirodipterus* (Campbell & Barwick, 1982).

Porolepiformes can be shown to be monophyletic by having dendrodont tooth structure (Schultze, 1970). In addition to this character, the presence of a prespiracular plate and preoperculosubmandibular bone may be further synapomorphies of the group. This leaves *Canowindra* to be placed phylogenetically in only one way: as a specialized osteolepiform which differs from all others by the unique pattern of the skull roof, subdivision of the postorbital bone and narrow shape of the jugal bone. Osteolepiform synapomorphies, such as the enlargement of the lachrymal bone and basal scutes at fin origins (Long, 1985), are not seen on *Canowindra*, and may be regarded as synapomorphies of osteolepids and eusthenopterids excluding *Canowindra*. *Canowindra* also differs from these two groups in the shape of the opercular which is a deep bone rather than being squarish or longer than deep. This character could be regarded as plesiomorphic on evidence from the taxonomic distribution of opercular shapes in primitive osteichthyans (Actinopterygii; Pearson, 1982). If cycloidal scales evolved only once within Osteolepiformes, then *Canowindra* could be placed as the sister taxon to eusthenopterids, but this hypothesis would assume that the osteolepiform synapomorphies not seen in *Canowindra* were independently acquired in osteolepids. The parsimonious alternative to this hypothesis is to place *Canowindra* as the sister taxon to osteolepids and eusthenopterids (Osteolepiformes *sensu stricto*) and expand the definition of the group to include *Canowindra*. This assumes that cycloid scales with a median boss on the basal surface evolved

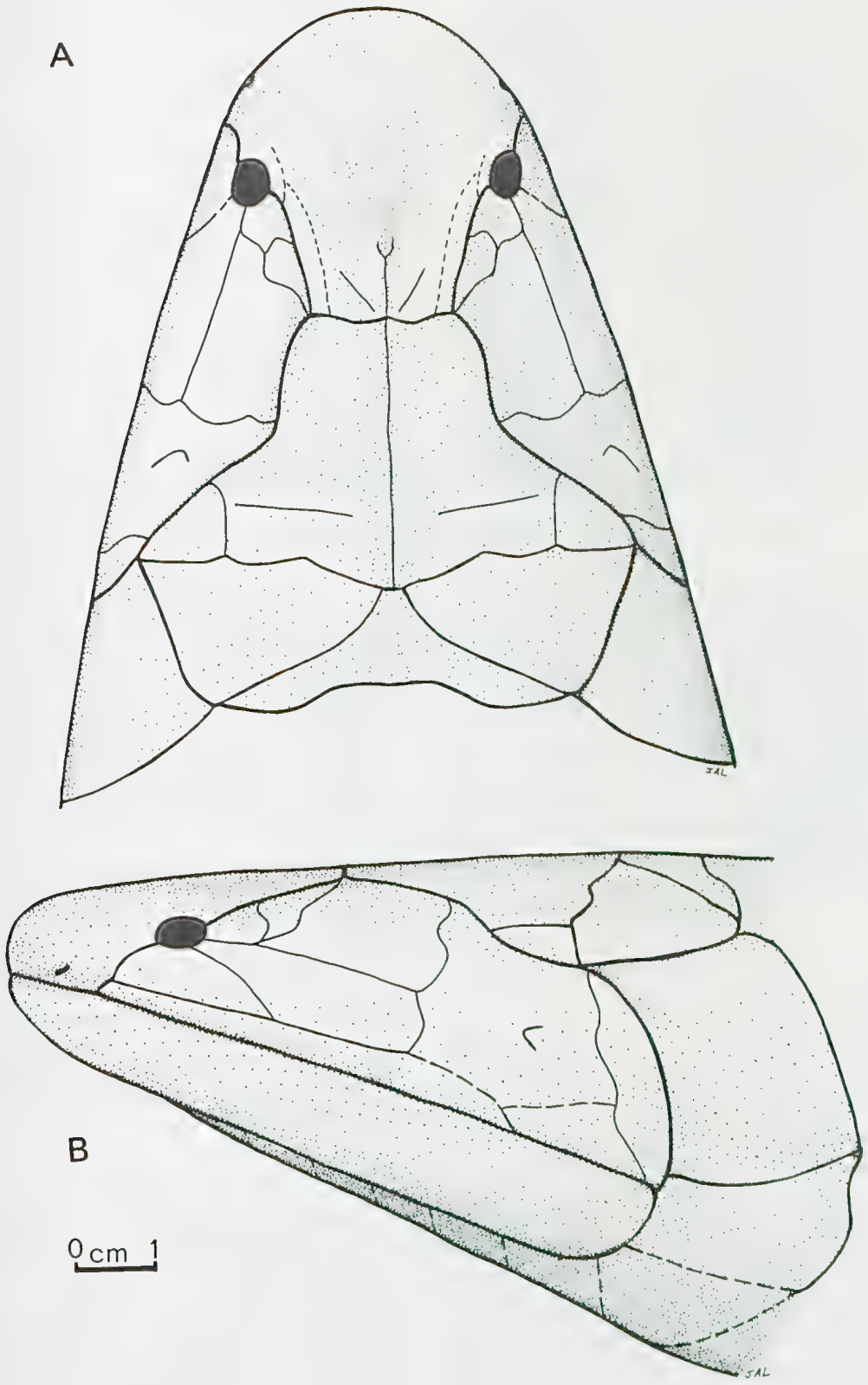

Fig. 5. *Canowindra grossi* Thomson. Attempted restoration of the head in **A**, dorsal and **B**, lateral views. After the holotype, Australian Museum F47153.

	A. Osteolepiformes	B. Porolepiformes	*Canowindra*
1. Parietal shield	Separate parietal, intertemporal and supratemporal bones	Fused parietal and intertemporal bones	Fused parietal, supratemporal and intertemporal bones
2. Parietal shield	Narrow	Broad	B
3. Frontal shield bones	Separate dermosphenotic	Dermosphenotics and frontals fused	?B
4. External nares	One pair	Two pairs	A
5. Orbit size	small-large	small	B
6. Extrascapulars	Median bone is overlapped by lateral bones	Median bone overlaps lateral bones	A
7. Postorbital	Single bone	Single bone	Three bones
8. Squamosal	Single bone	Multiple bones	A
9. Preopercular	Bar-like, verticle	Broad, squarish	A
10. Preoperculosub-mandibular	Absent	Present	A
11. Pectoral girdle	Anocleithrum large externally exposed	Anocleithrum small ?subdermal (Long, 1985)	A
12. Cycloid scales	With median boss on basal surface	Without median boss	A

Table 2. Comparison of character states of Osteolepiformes, Porolepiformes and *Canowindra grossi*

as parallellisms in *Canowindra* and eusthenopterids, as they did for holoptychioids, actinistians and higher dipnoans (Schultze, 1977). *Canowindra* should be placed in its own suborder equal in rank to the Osteolepiformes (Osteolepididae, Lamprotolepididae, Eusthenopteridae, ?Panderichthyidae, ?Rhizodopsidae). However, as there are other newly discovered osteolepiform-like fishes from the Devonian of Australia and Antarctica which share derived features with *Canowindra*, the task of erecting higher taxonomic levels will be postponed until the systematic descriptions of the other new forms are completed.

Formal Systematics

Canowindra grossi Thomson, 1973

Amended diagnosis. A moderately large, fusiform rhipidistian fish. Fronto-ethmoidal shield/parietal shield ratio 150. Orbits very small. Distance from tip of snout to beginning of first dorsal fin insertion approximately 4 times the combined skull table length; equal to 0.57 times total length of fish. Parietal shield comprises fused parieto-intertemporal-supratemporal bones separated by median suture; broad triangular extratemporals; breadth/length ratio 194. Cheek with single, large, squamosal, bar-like preopercular, and three postorbital bones dorsal to slender jugal. Lower jaw contained 6.8 times in length of fish. Lateral extrascapulars broader than long, almost meeting in midline. Opercular large, deeper than long. Pectoral girdle with large externally exposed anocleithrum, twice the size of scales; cleithrum with straight dorsal edge. Scales round with median boss on basal surface. Dermal bones and scales lack cosmine, ornamented with separate tubercles. Trunk with circular cross-section in front of dorsal fins; tail strongly heterocercal. Basal scutes absent from fin bases.

Holotype. AM F47153 (only specimen), kept in the Australian Museum, Sydney.

Age and occurrence. Upper Devonian Mandagery Sandstone (?Famennian, Long, 1983), collected near Canowindra, New South Wales.

ACKNOWLEDGEMENTS. The preparation of the holotype of *Canowindra* by Dr Alex Ritchie and Mr Robert Jones (Australian Museum, Sydney) resulted in the new cast of the head being available for me to study. I sincerely thank them for permitting me to redescribe this important fish, as well as for helpful discussion on the work. For reading the manuscript and offering helpful suggestions I thank Prof. Ken Campbell (Australian National University, Canberra). This work was carried out in the Geology Department, Australian National University, under the award of a Rothmans Fellowship.

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Additional Nereidids (Polychaeta) from Eastern Australia, together with a Redescription of *Namanereis quadraticeps* (Gay) and the Synonymising of *Ceratonereis pseudoerythraeensis* Hutchings & Turvey with *C. aequisetis* (Augener)

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Sydney South, N.S.W., 2000

Abstract. *Ceratonereis pseudoerythraeensis* Hutchings & Turvey, 1982, an extremely common estuarine nereidid throughout southern and eastern Australia, is synonymised with *Ceratonereis aequisetis* (Augener, 1913), previously only known from the Swan River, Western Australia. A new record of *C. amphidonta* Hutchings & Turvey, 1982, from South Australia is given from Victoria. *Namalycastis* cf. *abiuma* (Müller, 1871) is described. Material from the type locality of *Namanereis quadraticeps* (Gay, 1849) is described and compared to *N. littoralis* Hutchings & Turvey, 1982. The only known record of *Pseudonereis masalacensis* (Grube, 1878) from Australia is referred to *Pseudonereis anomala* Gravier, 1901.

Hutchings, P.A. & C.J. Glasby, 1985. Additional nereidids (Polychaeta) from eastern Australia, together with a redescription of *Namanereis quadraticeps* (Gay) and the synonymising of *Ceratonereis pseudoerythraeensis* Hutchings & Turvey with *C. aequisetis* (Augener). Records of The Australian Museum. 37(2):101–110.

Keywords: taxonomy, Australian polychaetes, estuarine nereidids, redescription, type-species.

In 1982, Hutchings & Turvey published a comprehensive study of the nereidids predominantly of South Australia, in which they described a new species of *Ceratonereis*, *C. pseudoerythraeensis*, belonging to a group characterised by giant, simple setae. Following publication of this paper, Dr Hartmann-Schröder drew the senior author's attention to the presence of such setae in *Ceratonereis aequisetis* (Augener) although Augener (1913) had made no mention of this type of simple setae in the description of the species. Examination of Augener's type confirmed that *C. pseudoerythraeensis*, an extremely common and widely distributed species, was identical with *C. aequisetis*. An additional new record of *Ceratonereis amphidonta* Hutchings & Turvey, 1982, from Westernport Victoria is given; the species was previously only known by a single specimen from South Australia. Some material of *Namanereis quadraticeps* (Gay) from the type locality became available to us and we have described and designated a neotype of *N. quadraticeps*, the type-species of the genus. A full description of *Namalycastis* cf. *abiuma* (Müller) from southern Queensland is given. *Namalycastis abiuma* (Müller) is described together with some comments on the genus. The single record of *Pseudonereis masalacensis* (Grube, 1878) from Australia was found to be misidentified and the material has been reidentified as *Pseudonereis anomala* Gravier, 1901.

The following abbreviations have been used in the text, Allan Hancock Foundation, Los Angeles (AHF), Australian Museum, Sydney (AM), Zoologisches Institut und Zoologisches Museum der Universität, Hamburg (HZM), Queensland Museum, Brisbane (QM), Universytet Wroclawski Muzeum Przyrodnicze, Warsaw (WM), Museum of Victoria, Melbourne (MV).

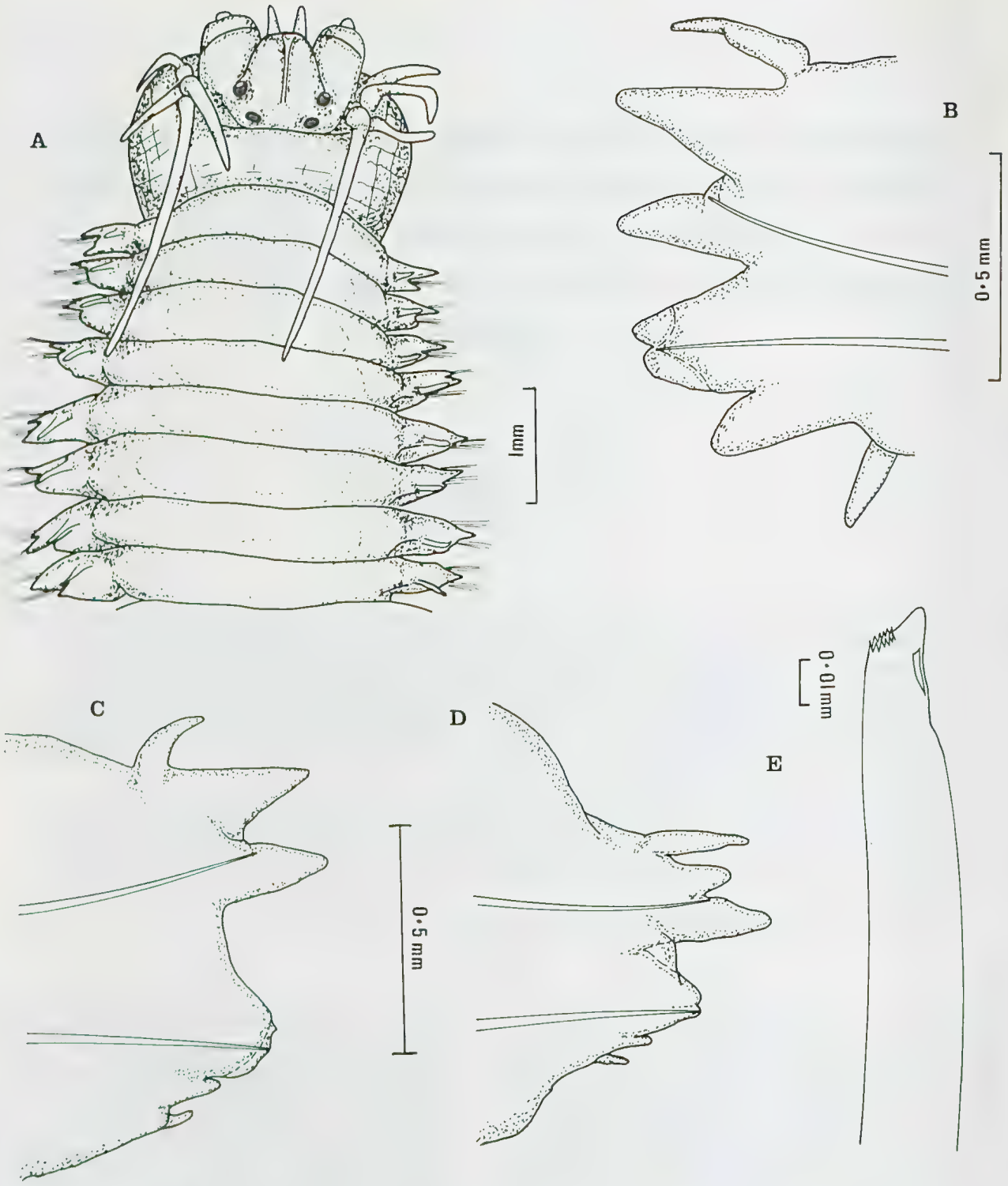

Fig. 1. *Ceratonereis aequisetis*: **a.**anterior end, dorsal view; **b.**left parapodium of setiger 9, posterior view; **c.**left parapodium of setiger 35, anterior view; **d.**left parapodium of setiger 68, anterior view; **e.**giant simple falciger from posterior parapodium. Setae omitted from figures of parapodia.

Ceratonereis aequisetis (Augener, 1913)
Fig. 1a–e

Nereis (*Ceratonereis*) *aequisetis* Augener, 1913: 171–174, pl. III fig. 48u, fig. 49u, text fig. 18a-c. — Hartmann-Schroder.
Ceratonereis near *anchylochaeta* Hartmann-Schröder, 1979: 112, fig. 183.
Ceratonereis pseudoerythraeensis Hutchings & Turvey, 1982: 98–102, fig. 2a–e. — Hutchings & Murray, 1984: 36.

Material examined. Material identified by Augener as *Ceratonereis aequisetis*, Western Australia, Swan R. Melville Water, St. 41, coll. 13-10-1905 (HZM V7918), 6 specimens, range of size of complete specimens (length mm/max width mm/nos of setigers) 38/3.5/90, 38/4.0/85, 58/4.5/96, 35/3.5/75. Specimen illustrated from same locality but separated (HZM P.17968); Harvey Estuary, sandspit, 11.6‰, coll. Hartmann-Schröder 4–11–1975 (HZM P.17129), 4 specimens, 2 ♂, 2 ♀.

Holotype of *Ceratonereis pseudoerythraeensis*, South Australia, Onkaparinga Est. (AM W.18510).

Description. Preserved specimens pale yellow in colour, some with light brown pigment on dorsum of first 14-17 setigers and on peristomium, prostomium and palps (Fig. 1a).

Body solid, widest mid-anteriorly, tapering slightly posteriorly, somewhat flattened dorsoventrally. Medial groove on dorsum ranging from deep to very shallow depending on degree of expansion caused by coelomic gametes, from setiger 17-22 and continuing to end of body; ventral medial groove throughout.

Prostomium width about equal to length, 2 pairs black eyes, approximately circular in outline, anterior pair slightly larger and further apart than posterior pair, lens visible in anterior pair and sometimes in posterior pair. Palps robust and conical with small spherical palpostyle, lateral groove across palpophore about ⅔ along length. Antennae extend to about level of palps. Four pairs of tentacular cirri: 1 and 3 equal in size, extend to mid peristomium, 2 extending to setiger 1 and 4 extending to setiger 2–8. Pharynx with pair of transparent, brown jaws with 7–8, 9–10 moderately developed teeth. Paragnaths brown, triangular cones, slight variation in size, arranged as follows: I = 4–8 in an irregular patch; II = an oblique block of 25/28, 32/37, 28/29, 24/25; III = broad transverse patch of 5–7 irregular rows, consisting of 53–58 cones; IV = reverse Y shaped crescent made of 38, 41, 41/41, 43/43 cones.

Parapodia with conical notopodial lobes; dorsal base of ventral notopodial lobe anteriorly with small rounded presetal lobe. Dorsal neuropodial lobe broadly conical, distally with 2 small lobes in anterior parapodia (Fig. 1b); a small supra-acicular lobe, a large subacicular lobe; well developed postsetal lobe absent. Ventral neuropodial lobe initially conical, reduced to a small tubercle by setiger 20–29. Anteriorly, all parapodial lobes similar in size; in middle setigers notopodial lobes similar in size (Fig. 1c), 1–3 times larger than dorsal neuropodial lobe; posteriorly, dorsal notopodial lobe posteriorly reduced; notopodial lobe remains 1–3 times larger than dorsal neuropodial lobe. Dorsal cirrus similar or slightly shorter in length to dorsal notopodial lobe except in far posterior setigers (Fig. 1d), ventral cirrus extending ⅓ to ½ way to tip of ventral neuropodial lobe throughout. Acicula black, brown at extremities. Setae consist of several types: notosetae are homogomph spinigers, neurosetae include homogomph spinigers, heterogomph falcigers and giant, simple falcigers from mid setigers onwards in the supra-acicular fascicle, and heterogomph spinigers and heterogomph falcigers in the subacicular fascicle. Some individuals possess a few homogomph spinigers in subacicular neuropodial fascicle. Giant, simple falcigers with few, poorly developed teeth above main fang (Fig. 1e). For details of ranges of number of setal types along the body, see Table 1. Pygidium with pair of ventrally produced anal cirri, slender extending over last 5–6 setigers.

Some of the individuals gravid females, with no development of epitoky. Glandular ridges developed across dorsum of setigers 27–39 in gravid females but no signs of epitoky.

Comments. Hartmann-Schröder has examined the type specimens of *C. aequisetis* (St. 41, V10081) which consist of 2 anterior ends and a single complete specimen (pers. comm.). The complete specimen is a gravid female which shows no sign of epitoky. Careful examination of this type reveals the presence of giant, simple falcigers. However, in many parapodia these have been damaged. Heterogomph falcigers are present from setiger 8, specifically in the supra-acicular fascicle of the neuropodia, and in the subacicular fascicle both heterogomph spinigers and falcigers are present. Hartmann-Schröder (1979) also compared these type specimens with the material examined by us (V7918), and she concluded that they are identical. She also synonymised *C.* cf. *anchylochaeta* from Port Hedland (Hartmann-Schröder, 1979) with *C. aequisetis*.

The type material of *C. aequisetis* does, therefore, not totally agree with the description given by Augener (1913). Augener does not mention the occurrence of giant, simple falcigers which, admittedly, are mainly broken in the material examined by him. Similarly, he reported that neurosetal heterogomph falcigers are absent except in far posterior setigers, whereas they are present even in anterior setigers of the type material. However, in all of the Augener material examined a large proportion of the setae are damaged; perhaps this explains why Augener overlooked these two groups of characteristic setae. Hutchings & Turvey (1982) accepted Augener's description and did not examine the type as it was felt that the giant, simple falcigers would be so conspicuous and that they could not be overlooked, and therefore *C. aequisetis* did not belong to the group of *Ceratonereis* with giant, simple falcigers. Hutchings & Turvey (1982) then described a series of species of *Ceratonereis* with simple falcigers, and subsequently Hutchings & Glasby (1982) and Ben-Eliahu *et al* (1984) described additional species. Hartmann-Schröder

brought it to our attention that *C. aequisetis* did, in fact, have simple falcigers and we then examined the series (V7918) and could not differentiate these specimens from *C. pseudoerythraeensis* Hutchings & Turvey, 1982. Therefore the latter species is here synonymised with *C. aequisetis*.

Ceratonereis aequisetis occurs widely throughout estuarine and shallow, protected coastal waters in Southern Australia. Hartmann-Schröder (1983) has also recorded it from a wide variety of estuarine habitats in Western Australia. Currently, this species has been only reported from Australia.

Augener's material is gravid but shows no sign of epitoky. Hutchings & Turvey (1982) reported that some of their material had been found in fine, sandy tubes surrounded by juveniles or eggs, with the females exhibiting no signs of epitoky, providing additional evidence that *C. pseudoerythraeensis* is synonymous with *C. aequisetis*.

Habitat. Protected bays and estuaries, sandy seagrass substrates or in mangroves; salinity range 9.9–35‰.

Australian distribution. Western Australia, South Australia, Victoria, New South Wales and Queensland.

Ceratonereis amphidonta Hutchings & Turvey

Ceratonereis amphidonta Hutchings & Turvey, 1982: 97–98, fig. 1a–c.

Material examined. Victoria, Westernport Bay, 1 (MV F50049).

Remarks. This single specimen agrees very well with the holotype of *C. amphidonta* which was described from South Australia. This is only the second reported specimen.

Habitat. *Posidonia* seagrass beds.

Australian distribution. South Australia (Maston Point, Kangaroo Island), Victoria (Westernport Bay).

Namalycastis cf. *abiuma* (Müller, in Grube, 1871)

Fig. 2a-g

Paranereis abiuma Müller in Grube, 1871: 47–49. — Hartman 1959a: 163-166, pl III. 1–4.
Namalycastis abiuma. — Russell, 1962: 6.

Material examined. Queensland, Serpentine Creek, Cribb Island, many (QM G7493-500); airport drain, Brisbane (QM G10705).

Description. Stout worm, all incomplete, range in size from 35 mm long, 3 mm wide (excluding parapodia) for 55 setigers to individuals 72 mm long, 4 mm wide for 130 setigers. Preserved material with dorsum, including prostomium and palps, uniformly brown pigmented. Some radiation in the intensity of pigmentation with material examined. Parapodia, including dorsal lobe, antennae, palpostyles of palps, tentacular cirri and ventrum, cream coloured.

Prostomium trapezoidal with short squat palps and small spherical palpostyles. Two small triangular antennae. Two pairs of dark, brownish eyes situated adjacent to one another at the lateral margins of the prostomium. Four pairs of short, stumpy tentacular cirri, longest pair barely extending beyond the posterior margin of the prostomium (Fig. 2a). Segment 1 narrow and achaetous.

Pharynx everted on some specimens (QM G7498), lacking any chitinous paragnaths or papillae. Pair of heavily chitinised dark-brown jaws, with 5-8 teeth arranged in a vertical row, terminal tooth slightly larger (Fig. 2b). Number of teeth similar within an individual but some variation within material examined.

Parapodia sub-biramous with 2 dark-brown to black acicula; noto-aciculum almost emergent. Notopodium absent, represented by large dorsal lobe; dorsal cirrus absent. Dorsal lobe initially triangular with a constricted terminal portion, constriction resembles an articulation; posteriorly the lobe becomes enlarged, lamellar and at least twice the length of the parapodium. Neuropodium consists of a pre- and postsetal lobe: presetal longer and bilobed, postsetal rectangular. Small, elongated, triangular ventral cirrus (Fig. 2c–e).

Notosetae completely absent; neurosetae include about 4 spinigers and 10 falcigers in each fascicle. Spinigers homogomph with long fine blades that are finely denticulate at the base (Fig. 2f). Falcigers heterogomph with finely denticulated blades, denticulations more pronounced at the base of blade. At point of articulation of blade onto shaft, slight extension of shaft to form a collar. Core of shaft strongly granular, and base of shaft with closely spaced transverse striations (Fig. 2g).

Under X10 magnification, parapodial dorsal lobe with a very prominent series of ducts arising from a larger, central medial canal. This complex arrangement of canals forms a three-dimensional network penetrating throughout the lobe. Similar ducts, but fewer in numbers, occur on the neuropodial lobe. Some individuals with gregarines attached to the external surface of the dorsal lobe. None of the material examined was gravid.

Comments. This species was collected from intertidal and subtidal muddy sediments in mangrove creeks which flow into Moreton Bay, southern Queensland. It seems likely that the well developed ducts observed running through the dorsal and neuropodial lobes are blood vessels, although all the preserved material had colourless parapodia. If this is the correct interpretation, then the almost foliaceous dorsal lobes must considerably facilitate oxygen uptake in an environment low in oxygen. Some other genera of nereidids reported from mangroves, for example *Dendronereis*, have parapodial branchiae which presumably facilitate oxygen uptake.

Discussion. This species has only been recorded from Moreton Bay, Australia (Russell, 1962) the same area from which the present material was collected.

This species was initially described by Müller (1871) from Brazil, and the description is very brief. Hartman

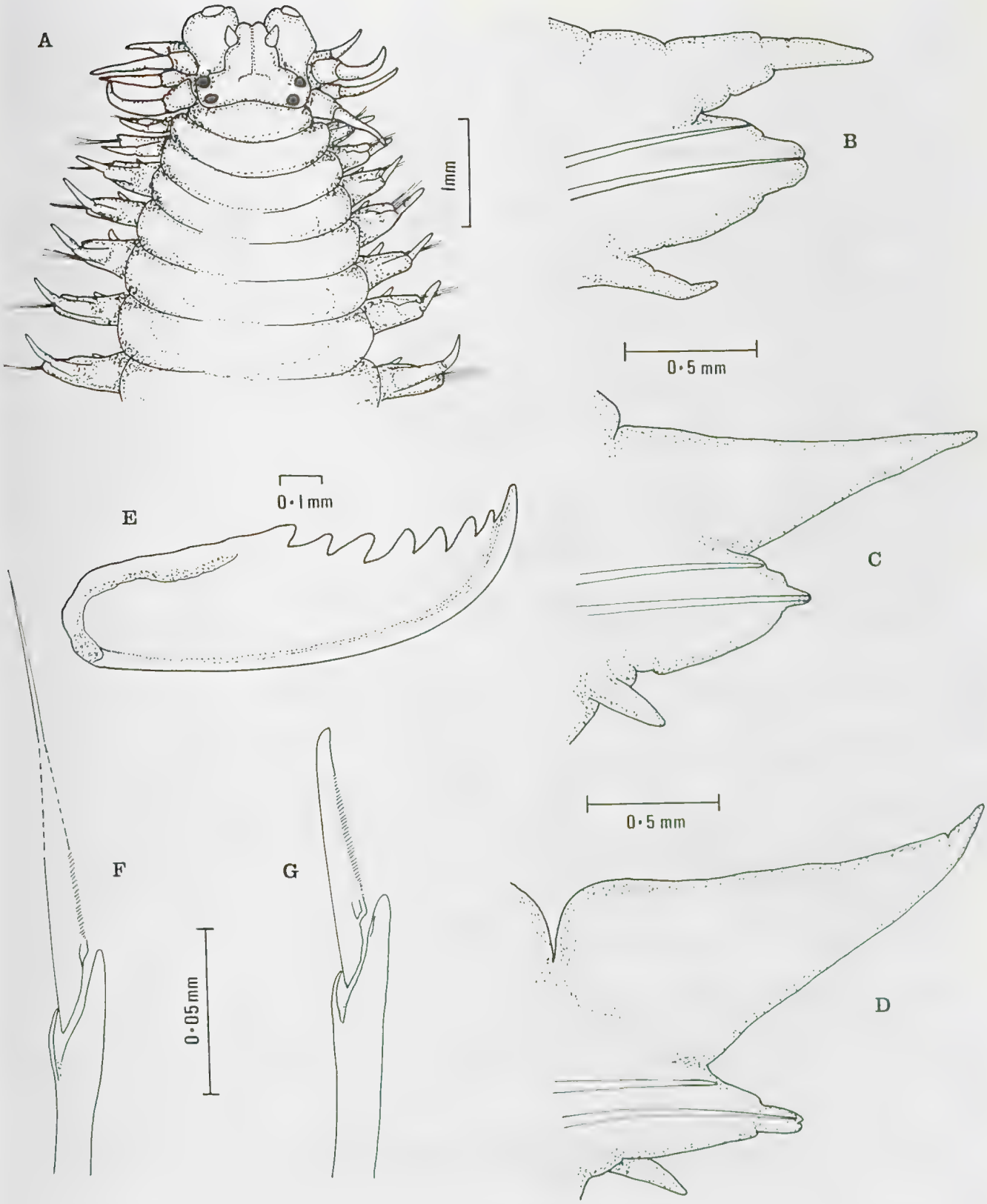

Fig. 2. *Namalycastis* cf. *abiuma*: **a.**anterior end, dorsal view; **b.**left parapodium of setiger 9, anterior view; **c.**left parapodium of setiger 54, anterior view; **d.**left parapodium of setiger 121, anterior view; **e.**right jaw, ventral view of concave surface; **f.**heterogomph spiniger; **g.**heterogomph falciger. Setae omitted from figures of parapodia.

(1959a), in a review of freshwater nereidids, synonymised 11 species with *N. abiuma* although, from her comments, it seems unlikely that she examined any of the material. These 11 species were described from scattered localities around the world and it is difficult to conceive how they could, in fact, be just one species, for many were recorded from isolated freshwater or brackish water environments.

The material from south-eastern Queensland has been fully described as it is probably not *N. abiuma* Müller but, before describing it as a new species, the type material, or at least material from the type locality of *N. abiuma* together with type material or material from the type locality of all the species synonymised by Hartman (1959a) with *N. abiuma*, should be examined. Separation of these species, if they are in fact different, may be very difficult as this genus lacks the characters commonly used to separate nereidid species. These characters are the ornamentation of the pharynx, complex parapodial lobes and the type of notosetae present.

Many other estuarine or brackish water habitats have been examined along the east coast of Australia, and to date this is the only locality from which this species has been recorded. This species is the only representative of the genus found in Australia.

Habitat. Estuarine creeks lined with mangroves.

Australian distribution. Southern Queensland.

Namanereis quadraticeps (Gay, 1849).
Fig. 3a–e

Lycastis quadraticeps Gay, 1849: 24 (in Blanchard, 1849). – Ehlers, 1897: 70; 1900: 214–215; 1901: 121; 1913: 498.

Material examined. Chile, *Metula* oil spill study, Straits of Magellan just north of Bahia San Gregorio. Coll. D. Straughan Jan. 1977. Neotype (AM W.198509). Voucher material from the same locality as the neotype has been deposited in (USNM 097377), (BMNH ZB 1984.52–53) and (AM W.198510). Magellan Straits Punta Arenas; beach under stones (HZM V4780) det. Ehlers.

Additional material. Santa Rosalie, Bahia, Southern California (AHF).

Description. Complete individual, 1 cm long, 1 mm wide, 50 setigers. Preserved body pale cream in colour. Prostomium bluntly triangular with pair of small, blunt antennae. Pair of bulbous, biarticulated palps with small, rounded palpostyles. Four pairs of short, tentacular cirri with swollen bases. Two pairs of semi-circular eyes, hidden by prostomial fold (Fig. 3a).

Pharynx dissected. Pair of lightly chitinised jaws with 7 lateral teeth. Chitinous paragnaths and papillae absent.

Parapodia sub-biramous with dark brown acicula. First setiger occurs on the segment following the tentacular cirriferous segment. Small dorsal cirrus rounded; elongated neuropodia with almost equal sized pre- and postsetal lobes; small, globular ventral cirrus. Parapodia similar along entire body (Fig. 3b). Notosetae consist of a single heterogomph spiniger with finely denticulated blade in each parapodium (Fig. 3c-d). Neurosetae consist of a single heterogomph spiniger and about 6 heterogomph, short-bladed falcigers, with strongly toothed blades. Shaft of falciger with strongly granular core (Fig. 3e).

Pygidium, a rosette with at least one small, triangular anal cirrus, presumably originally paired.

Comments. Variations exhibited in the other material (18 anterior fragments plus some posterior fragments) consist almost entirely of intensity of eye pigmentation. Material, that is all similar in size, is not gravid. Posterior fragments have a pair of anal cirri.

The material identified by Ehlers as *N. quadraticeps* closely resembles the type series, however the specimens are slightly larger, setiger to length (mm), 65, 25; 57, 16; 55, 13.5; 52, 15 and 44, 14.5.

Discussion. The type-species of *Namanereis*, *N. quadraticeps* (Gay), was described in 1849 from Calbuco, Chile. Gay originally described his species as *Lycastis quadraticeps*. However, the name was preoccupied and Chamberlin (1919) proposed the new name of the genus *Namanereis* with *N. quadraticeps* as the type-species. The description is very brief and no type material is presumed to have been deposited. Subsequently, the species was recorded by Ehlers (1897, 1900, 1901 and 1913) from the Straits of Magellan in 2.7 fms; Punta Arenas intertidally; and St Paul, Ebbestrand – all in South America. Ehlers provides no descriptions. Benham (1909) also described *N. quadraticeps* from Campbell Island, and Augener (1924) subsequently reported the same species from Port Ross, Auckland Island which is in the same biogeographic areas as Campbell Island. Hutchings & Turvey (1982) synonymised Augener's and Benham's material with *Namanereis littoralis* Hutchings & Turvey which they described from intertidal areas of eastern Australia.

Hartman, in 1959b, synonymised *Lycastopsis beumeri* Augener, 1922, with *N. quadraticeps* following Wesenberg-Lund's (1959) synonymy of *Lycastoides pontica* (Bobretzky, 1870 or 1881) with *L. beumeri*. Bobretzky's description of material from the Black Sea, either in 1870 or 1881, was in Russian and unavailable to Wesenberg-Lund and to the present authors. In her synonymy, Wesenberg-Lund utilised the drawings of La Greca (1949) of *L. pontica*. It therefore follows that *L. pontica* is also synonymous with *N. quadraticeps*. Hartman (1968), realising this, although not referring to it in the text, used La Greca's drawings of *L. pontica* in her description of *N. quadraticeps* from southern Calfornia. The figures of La Greca and the description of Wesenberg-Lund clearly indicate that only 3 pairs of tentacular cirri are present.

Material from Chile collected by Straughan and examined by us, has four pairs of tentacular cirri, and this material agrees with that of Ehler's which we have examined. We therefore propose to designate a neotype from the material collected by Straughan, and have redescribed the species.

Material from southern California has been examined

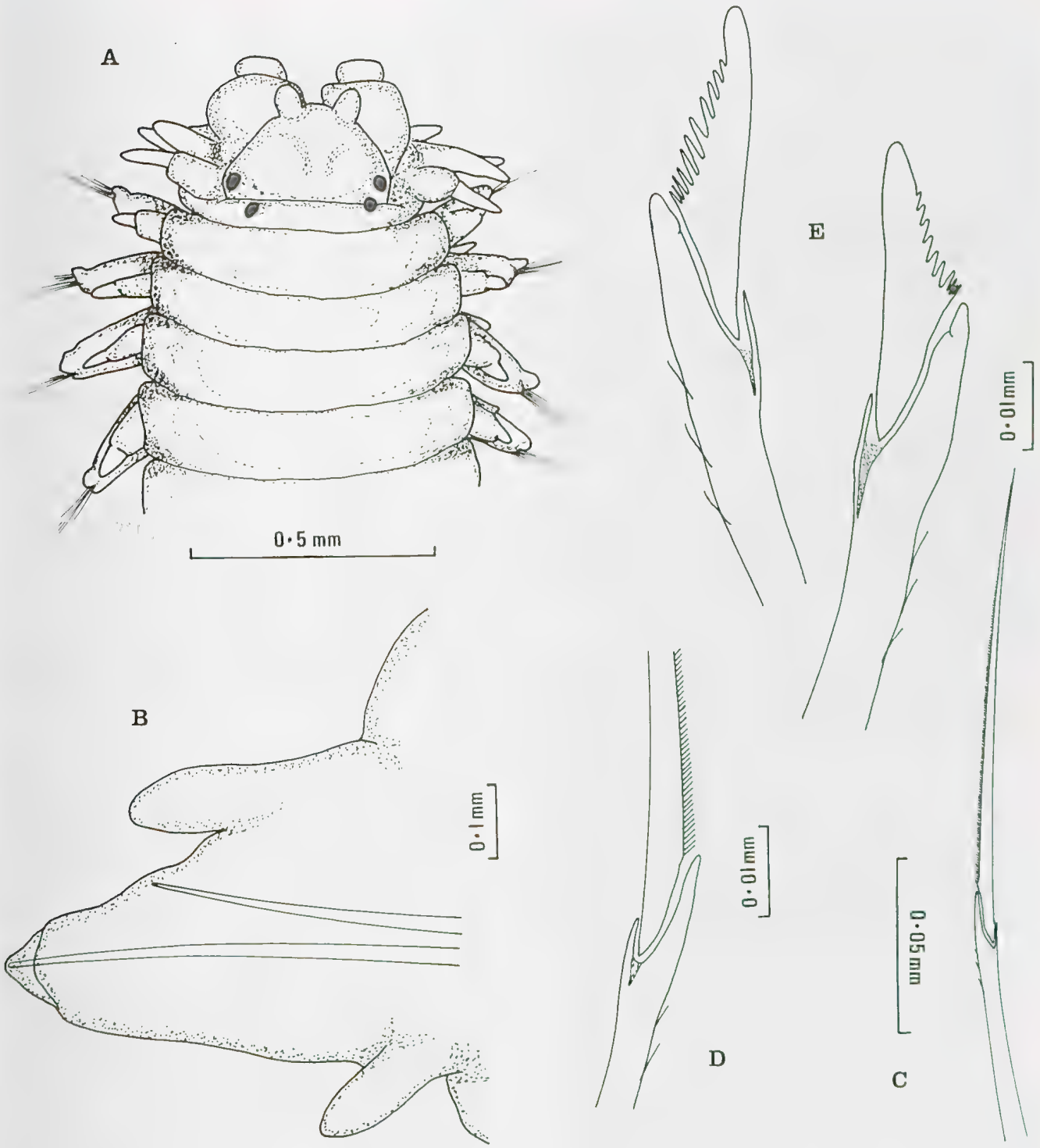

Fig. 3. *Namanereis quadraticeps*, neotype: **a**.anterior end, dorsal view; **b**.right parapodium of setiger 12, anterior view; **c,d**.neuropodial heterogomph spiniger from setiger 12; **e**.neuropodial heterogomph falciger from setiger 12. Setae omitted from figures of parapodia.

and agrees closely with that of Hartman's (1968) description, and we suggest that this is not *N. quadraticeps* Gay but is another, possibly undescribed species of *Namanereis*. Fauchald's (1977) definition of the genus states that the genus may have 3–4 pairs of tentacular cirri and that the notopodial lobe is poorly developed so that the Californian material certainly does belong to the genus. Notosetae are completely absent from the southern Californian material, whereas a single one is present in *N. quadraticeps*.

Thirteen species have been tentatively assigned to the genus *Namanereis* by Hartman (1959a) and since then only one additional species *N. littoralis* Hutchings & Turvey, 1982, has been described. Hartman (1959a, b) also suggests that many, if not all, of the 13 species are synonymous with *N. quadraticeps*. However, many of these species occur in isolated areas of the world, and it seems unlikely that we have a widely distributed cosmopolitan species. Certainly Hartman's record from southern California is in doubt. A detailed study of this genus is urgently needed.

Namanereis quadraticeps can be separated from *Namanereis littoralis* Hutchings & Turvey,1982, by the almost emergent neuro-aciculum in *N. quadraticeps* (in *N. littoralis* it is completely submerged), and by subtle differences in the articulation of the falcigers and spinigers which are strongly heterogomph in *N. quadraticeps* and only weakly heterogomph in *N. littoralis*. Finally, there are slight differences in the shape of the postsetal lobes and in the prostomium. The prostomium in *N. quadraticeps* is broadly T-shaped, whereas in *N. littoralis* it is almost rectangular. The postsetal parapodial lobe in *N. quadraticeps* is more pointed than in *N. littoralis*. However, it is recognised that the two species are very similar. As already commented on in the discussion of the species of *Namalycastis*, these genera of nereidids which lack any of the traditionally used features to separate species may be extremely difficult to define and we may have to be reliant on ecological data or differences in reproductive methods to separate the species.

Habitat. Intertidal, mixed sediments with surface cobbles and intervening sand and gravel. Kelp also present.

Distribution. Chile, Straits of Magellan.

Pseudonereis anomala Gravier, 1901

Pseudonereis anomala Gravier, 1901: 191–197, pl. 12, figs 50–52. – Fauvel, 1911: 395–397; 1922: 494. – Hutchings & Turvey, 1982: 141-142.

Pseudonereis masalacensis. – Pope, 1943: 244. Not Grube.

Material examined. *Pseudonereis anomala*: Western Australia – Houtman Abrolhos, Pelsart Is., 1(AM W.4862); Rottnest Is., mangroves (AM W.4863); Freemantle, 9(AM W.18476); Cowaramup Bay, 1(AM W.4864-65); Albany, 2(AM W.4861). South Australia – Kangaroo Is., Maston Pt, 1(AM W.18313), Cape du Couedic, many (AM W.18310-12). New South Wales – Manly, 4(AM W.4316); Long Reef, 1(AM W.4357); 2(AM W.3219), 2(AM W.4860), collected E.C. Pope, 1938.

Additional material. *Nereis* (*Lycoris*) *masalacensis*, Masolac, Philippines, Holotype (WM311).

Comments. Pope (1943) reported *Pseudonereis masalacensis* from Long Reef, Sydney, and incorrectly cited *P. masalacensis* as having been described by Fauvel instead of Grube (1878). We questioned the identity of this material as this species has not been recorded from Australia before or since the Long Reef survey, despite extensive collections in at least the eastern and southern parts of Australia. Therefore we examined the type of *P. masalacensis*.

The holotype of *Pseudonereis masalacensis* (Grube) is considerably flattened, distorted and, as a result of preservation in formalin, in very poor condition. The numbers and arrangement of paragnaths are generally very difficult to interpret, and paragnaths in Areas VII–VIII are not visible at all. The setae have lost most of their rigidity and are often broken between the shaft and the blade. Grube, unfortunately, does not give an adequate description of the setae. As paragnath patterns and the distribution and types of setae are now recognised as important characters in nereidid taxonomy we therefore suggest that this species is essentially indeterminable unless additional material can be collected from the type locality.

Pope's material was compared to the holotype of *P. masalacensis*, and we found distinct differences in the shape of the posterior notopodial lobes. The holotype shows no posterior changes in the shape of the notopodial lobes, whereas the Long Reef material, especially the larger specimens, shows considerable dorsolateral elongation of the dorsal notopodial lobes in posterior setigers. In this respect Pope's material closely resembles *P. anomala* Gravier. Other authors have, in fact, used this character, along with the paragnath arrangement in Area VI, to facilitate the separation of *P. anomala* from *P. masalacensis* (Gravier, 1901; Fauvel, 1911).

The number of paragnaths is generally fewer in Pope's material than is given in previous descriptions of *P. anomala*, although the characteristic arrangement of paragnaths in regular, comb-like rows in Areas II, III, IV appears very similar. In Area VI, however, Pope's material has 10–18 cones in 2–3 irregular transverse arcs compared to a single transverse arc of 6 cones in Gravier's description, and a single, transverse arc of 5–9 cones in Hutchings & Turvey (1982). Other specimens examined showing a departure from the single arc of paragnaths in Area VI include one from Pelsart Is., Abrolhos, North West Australia (AM W.4862) which has 6 cones in 1 arc on one side, and 6 comes in 2 arcs on the other side, and one specimen from Cape du Couedic (AM W.18312) which has 6 cones in 1 arc on one side, and 9 cones and 1 short bar in an irregular patch on the other side. In addition, Fauvel (1922) reports a specimen, also from Pelsart Is., with one transverse row of paragnaths, tending to divide into two.

Considering these variations in paragnath pattern in Area VI, and the considerable variation in paragnath numbers previously attributed to the species (Hutchings & Turvey, 1982), the variation exhibited in Pope's material would seem acceptable. We therefore reassign Pope's material to *P. anomala*. Certainly, in all other respects, Pope's specimens appear identical to Gravier's description of *P. anomala* and to the material examined by Hutchings & Turvey. The only other species of *Pseudonereis* recorded from Australia, *P. rottnestiana* Augener, 1913, displays the characteristic leaf-like expansion of the dorsal notopodial lobe in posterior parapodia, like *P. anomala*, but differs in having far fewer paragnaths in the maxillary ring.

Habitat. Associated with encrusting fauna, coralline algae and algal holdfasts.

Australian distribution. Western Australia, South Australia and New South Wales.

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	Ant. Setigers	Mid Setigers	Post. Setigers
Notosetae:			
homogomph spinigers	8–17	4–10	3
Neurosetae:			
Supra homogomph spinigers	5–14	2–8	4–5
heterogomph falcigers	2–5	0	0
giant, simple falcigers	0	1–2	1–2
Sub heterogomph spinigers	3–18	4–6	1–2
heterogomph falcigers	2–3	3–5	2–3

Table 1. Distribution of setal types in the type series of *Ceratonereis aequisetis*.Many of the setae damaged, especially posteriorly and several individuals posteriorly incomplete, so some counts are underestimates of setal types presented.

A female Noisy Scrub-bird *Atrichornis clamosus* at nest (photo G. Chapman, CSIRO Wildlife Research).

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NATURAL HISTORY

Morphology of the Noisy Scrub-bird, *Atrichornis clamosus* (Passeriformes: Atrichornithidae): Introduction, with Remarks on Plumage and Systematic Position

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ABSTRACT. A brief review is given of previous morphological studies of *Atrichornis* and its relationship to other passerine families. Renewed interest in the relationships of *Menura* and *Atrichornis* in the last two or three decades led to efforts to obtain suitable specimens of both genera. The efforts to obtain the specimen of the rare *Atrichornis clamosus* used in this study are described in detail. This account highlights the long periods necessary to obtain governmental permission to study an endangered species and suggests that *bona fide* scientific enquiry can be stifled by unyielding governmental regulations designed to regulate commercial trade. The studies in this volume illustrate the wealth of scientific data that can be obtained from a single specimen in a carefully co-ordinated study.

CLENCH, M.H. & G.T. SMITH, 1985. Morphology of the Noisy Scrub-bird, *Atrichornis clamosus* (Passeriformes: Atrichornithidae): introduction, with remarks on plumage and systematic position. Records of the Australian Museum 37(3): 111–114.

KEYWORDS: Atrichornithidae, endangered species, governmental regulations, Menuridae, morphology.

Within the uniquely Australian avifauna, the two species of scrub-bird (*Atrichornis*) are unquestionably among the most intriguing. Found in restricted ranges on opposite sides of the continent, scrub-birds have long been ornithological enigmas. Because they live in exceptionally dense habitat, are terrestrial and cryptically coloured, they are notoriously difficult to see — even when you know, from the loud and persistent song, that a bird is somewhere within a few metres of you. Many professional ornithologists and amateur bird-watchers alike have spent hours sitting or crouched in a spot, with a bird moving about and calling all around them, without catching even a glimpse of the small brown form. Accordingly, until intensive study was begun by the C.S.I.R.O. on the Noisy Scrub-bird in recent years, almost nothing was known of the details of distribution, ecology, behaviour, or even many of the basic facts of the life histories of these birds — and much still remains to be learned (Chisholm, 1951).

The Noisy Scrub-bird (*Atrichornis clamosus*) was first discovered by J. Gilbert in 1842, and described formally in the scientific literature two years later by J. Gould (1844). Gould's original generic name, *Atrichia,* was later found to be preoccupied (Stejneger, 1885) and altered to the present spelling. The species occurred in south-westernmost Western Australia, and was recorded occasionally in the coastal region between Perth and Albany until late in the 19th century (localities mapped by Smith, 1977). After 1889 it was not seen (or, to be more realistic, heard) again for many decades and was presumed to be extinct. Its rediscovery by H. O. Webster in 1961 at Two Peoples Bay, some 40 km east of Albany, electrified the ornithological world (Serventy, 1966). Since that time, the Noisy Scrub-bird population has increased from 40–45 singing males (the population statistic) (Smith & Forrester, 1981) to 138 in 1983 (Smith, unpublished data). It is a species clearly still in need of continued study and help, if it is to be saved.

The Rufous Scrub-bird (*Atrichornis rufescens*) was described in 1866 by E. P. Ramsay. It was originally found in several isolated areas in south-eastern Queensland and north-eastern New South Wales.

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Although its range has since constricted (Smith, 1977), it still occurs in several montane localities within the same general region. *Atrichornis rufescens* is also a rare bird. Although its population is somewhat larger than that of *A. clamosus,* it is similarly of concern to conservationists and ornithologists. Its distribution and habitat requirements have been studied in detail by Simon Ferrier (pers. comm.). Other facets of its ecology have been little studied.

For several decades after scrub-birds first became known to science, studies of their taxonomy were based solely on the external features visible in museum study skins. Although both J. MacGillivray and Ramsay had superficially examined and noted several anatomical peculiarities in *Atrichornis,* neither communicated their findings (Chisholm, 1951). Gould (1865) assumed scrub-birds to be closely related to the superficially similar bristlebirds (*'Sphenura'* = *Dasyornis*), but commented on the curious lack of rictal bristles in *Atrichornis,* considering that they were such a characteristic feature in the other genus.

It was not until the first anatomical material was studied (Newton, 1875; Garrod, 1876) that *Atrichornis* was found not to be related either to other small brown Australian birds (especially certain malurines or timaliines) or to the South American tapaculos (Rhinocryptidae). Instead, the only group that shared distinctive morphological characteristics with *Atrichornis* were the equally anomalous lyrebirds (*Menura*). Lyrebirds (two species) are also Australian, but are so large-bodied that not until their anatomy was studied in the 1840's, were they proved to be passerines (perching birds) rather than some form of pheasant or other galliform. Although definitely passerine, *Atrichornis* and *Menura* were so different from other perching birds that Garrod (1876) erected a special small taxonomic grouping just for them: the 'Acromyodi Abnormales.' This was in contrast to the 'Acromyodi Normales' which constituted the thousands of species of true songbirds.

Since Garrod's dissection of an anatomical (spirit) specimen of *Atrichornis rufescens,* few morphological studies have been conducted to solve the puzzle of the relationships of this pair of Australian genera. Clearly, they were different from all other perching birds in several important features, notably in the structure of the syrinx, sternum and clavicles. Largely, however, through a lack of available specimens (Forbes, 1881), together with a general waning of interest in avian anatomy after the turn of the century, the enigma remained. Taxonomists continued, of course, to propose new systems of classification, but they merely reinterpreted the sparse existing data on *Atrichornis* and *Menura.* The taxonomic history of these genera was summarized by Sibley (1974) and is discussed in detail in the concluding paper of this monograph. It is sufficient to note here that, for the past century, *Atrichornis* and *Menura* have remained classified together (and with no other close relatives) somewhere just outside the true songbirds. They are most generally accepted as constituting the Suborder Menurae, placed just before the true songbirds, Suborder Passeres, of the Order Passeriformes (Wetmore, 1960).

THE PRESENT STUDY

In the past two or three decades, there has been a renewed interest in avian morphology, particularly in studies that might help to solve persistent systematic puzzles. With the long hiatus in anatomical work, however, many key specimens either no longer exist, or were never acquired during the routine growth of museum collections. In 1966 an attempt was made to locate the few skeletons and spirit specimens that had once existed of *Atrichornis* and *Menura.* Apparently the specimens in England either had been lost or destroyed by the London bombing during World War II (Chisholm, 1951; Heimerdinger & Ames, 1967). The only pertinent material located was four skeletons and two spirit specimens (in alcohol) of *Menura* (both the latter being partly grown nestlings, one much-dissected in the National Museum of Natural History, Washington, D.C., and the other, still unstudied, in the Royal Scottish Museum, Edinburgh), and a spirit specimen of *Atrichornis clamosus* (in the Museum of Victoria, Melbourne; Reg. no. R11354).

The *Atrichornis* specimen is very old. It is undated, but was received in Melbourne in 1889; it may be the specimen collected that year by A.J. Campbell (Chisholm, 1951). Apparently it originally was preserved in rum (a poor preservative but commonly used in remote collecting localities in the early years) and may have been prepared as an anatomical specimen because it was badly shot-damaged and would have been difficult to make into a study skin. The muscles are hard, the bones somewhat cleared and softened after nearly a century in fluid, and parts of the specimen were further destroyed by an attempt, in 1927, to determine the sex internally. Studies of its pterylosis and syrinx were conducted, with varying degrees of success (Clench, 1985; Ames, 1971).

Efforts were begun to acquire new spirit specimens of both genera, as the existing material was not even minimally satisfactory. Through the cooperation of several Australian ornithologists and the appropriate Australian authorities, a few specimens of *Menura* were preserved and made available for study. The comparisons within the Menurae in the following papers are primarily based on a well prepared pair of *M. novaehollandiae* obtained by Carnegie Museum of Natural History through the courtesy of H. J. deS. Disney and the Trustees of The Australian Museum, Sydney. Acquiring an *Atrichornis* was not so easy.

At the urging of several colleagues not directly involved, we have summarized here some of the many steps involved in the *Atrichornis* specimen acquisition. This account may serve as an example (perhaps an object lesson) to scientists, both to point out the very long periods of time necessary to obtain governmental permission to study a regulated species, and to suggest

that *bona fide* scientific inquiry can be stifled by unyielding governmental regulations formulated to control commercial trade. Truly, one must be both patient and persistent if one wishes to study a species that has been formally designated as endangered. As a result, too many discouraged scientists are abandoning such studies — to the detriment of the species being protected. Our saga also points out what can be accomplished with the sacrifice of just one individual bird.

At the International Ornithological Congress in Canberra in 1974, Clench and Smith informally discussed the possibilities of obtaining a spirit specimen of *Atrichornis*. As Smith was engaged in a long-term study of *A. clamosus*, and had shown that the population was increasing, it appeared reasonable to request permission to collect a single specimen. It was decided to collect a breeding female as such birds are the easiest to capture alive and, from the knowledge of the non-breeding population, it could be assumed with a high degree of confidence that she would be replaced by the following season and thus not affect the breeding population. Convinced of the importance of such a study, the governmental agencies charged with the protection of rare birds (Western Australian Wildlife Authority, Western Australian Department of Fisheries and Wildlife) issued the necessary collecting and export permits. Accordingly, on 15 August 1976 at 1330 hours, under conditions of gale force winds and biting sleet (fortunately not an omen) L.A. Moore snared a breeding female Noisy Scrub-bird at her nest 1.6 km north-east of Mt. Gardner, Two Peoples Bay (40 km east of Albany), Western Australia: 35°00′S, 118°10′E. The female chick from the nest was taken to Perth that night to form part of a small group (three females, one male) of birds to be used in an attempt to breed the species in captivity.

Before preservation, blood was drawn for later study by C. G. Sibley. The bird was also photographed and the following data taken:

Measurements: weight, 34 g; length of right tarsus, 27.5 mm; length of right wing (flattened wing chord), 63.6 mm; length of exposed culmen, 16.2 mm; overall length of body + tail, 190 mm.

Soft part colours: upper mandible dark greyish brown including operculum, tomium pale silvery pink from gape to near tip (which is the same as the remainder of the upper mandible); lower mandible pale silvery pink; mouth with palate very pale whitish pink, lining of upper mandible very pale grey, lining of lower mandible very pale greyish pink, upper surface of tongue white-cream; eye dark brown; eye ring greyish black; legs pale silvery grey; toes like legs but slightly darker; claws greyish white, darker on ridges.

After the 12 Australian permits were issued, Clench applied to the U.S. Fish and Wildlife Service for an import-export permit, to borrow the specimen for a cooperative study by American anatomists. Because the Noisy Scrub-bird is listed as an endangered species under U.S. law, and because the permit-issuing agency was undergoing an internal reorganization when the application arrived in Washington, the permit took almost five months to obtain. Several more months then passed while arrangements were made with U.S. Customs and a California broker; the package would contain an endangered species so it had to pass Customs at one of the few 'designated ports' — not Pittsburgh, where the specimen was to be studied first. This was such an important and irreplaceable specimen, we went to great lengths and considerable expense to ensure its safe journey.

It did arrive, safely, in March 1977. The sequence in which the specimen would be studied was predetermined, so that each anatomist could do his or her work without damaging the bird for those who would follow. Before the initial dissection, the specimen was photographed whole, to record the external morphology. The study then began with Morlion (who had travelled to Pittsburgh from Belgium) examining the wing and tail pterylosis. Clench followed with the body pterylosis. Raikow then studied several aspects of the external morphology (including a functional analysis of the locomotor apparatus) and the appendicular myology. As soon as the latter dissection was far enough along to disarticulate one wing and one leg, the rest of the specimen was carried to Washington where Zusi studied the myology of the trunk. Again, when the dissection was far enough advanced to disarticulate the head, it was carried to New York for Bock to begin on the jaw musculature and skull morphology. At this time the syrinx was removed and sent to P.L. Ames, and the stapes sent to A.J. Feduccia. After the dissections were completed, some of the now-cleaned bones were sent to the University of Kansas, for casting. Replicas of parts of the skeleton were made after permission was received from Australia to do so, and with care not to damage the bones. By using a casting technique developed for small fragile fossils, the replicas were made for distribution to several museums with major skeleton collections. Casts ('slabs') showing positive impressions of various elements have been deposited at the American Museum of Natural History, the British Museum (Natural History), the Royal Ontario Museum, the University of Michigan Museum of Zoology, the University of California Museum of Vertebrate Zoology, the U.S. National Museum of Natural History, the University of Kansas Museum of Natural History, Carnegie Museum of Natural History and the Australian Museum. These casts include the following elements (in some cases more than one view is shown): humerus, carpometacarpus and phalanges, femur, tibiotarsus, tarsometatarsus, all toes, and coracoid. Additionally, casts of the distal and proximal ends of some elements and of the more delicate ulna, scapula and synsacrum are on deposit at the Kansas Museum of Natural History. A cast of the synsacrum is also at the U.S. National Museum of Natural History. This distribution of casts means that at least some skeletal representation of *Atrichornis* will be available to scientists outside Australia — without an international

loan that currently means long delays, special permits and governmental red tape.

Throughout this study, Smith served as coordinator in Australia, Clench in the U.S. After the specimen arrived in the U.S., two additional permits were required. One was to re-export the specimen to Australia under the then-new Convention on International Trade in Endangered Species of Wild Fauna and Flora (CITES), which was implemented in the U.S. only a month after the specimen arrived. The other was an extension of the original permit — necessary because the cooperative study expanded to include study of other morphological systems after the bird was collected. It took more time than originally anticipated to complete the full round of dissections with the extra workers: everyone involved approached their tasks with unprecedent care. We knew that the *Atrichornis* was a unique specimen — an opportunity to study a key genus in avian systematics that might never again be available.

In December 1978, the specimen, now partially disarticulated and 'down to bare bones' on one side, but relatively intact on the other, was returned to its country of origin and incorporated into the collections at the Western Australian Museum (A15926). During this period we also completed the formal reports required on each of the permits issued.

Those who shared in the study of this exceptional species would like to thank all who cooperated in the project, especially the officials who issued the necessary permits with as much speed as could be managed. In many ways the following set of papers is a memorial to 'Upper Coffin' (whose territory was at the top of Coffin Gully), who contributed her all to science.

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Body Pterylosis of *Atrichornis, Menura*, the 'Corvid Assemblage' and Other Possibly Related Passerines (Aves: Passeriformes)

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ABSTRACT. In a study of the body pterylosis of *Atrichornis clamosus* and *Menura novaehollandiae*, the dorsal and ventral feather tracts of these taxonomic enigmas are compared with the pterylae of 96 other passerine genera in an effort to discover relationships. I conclude that scrub-birds and lyrebirds are each other's closest relatives but that the degree of similarity is such that they should remain separated taxonomically, at least in different families. Their next closest relationships lie with the Paradisaeidae-Ptilonorhynchidae-Callaeidae complex; the degree of similarity is not strong, but it is stronger than it is to any other passerine group.

Other major conclusions of this study are that: 1) the so-called 'corvid assemblage' is not a natural group; 2) *Astrapia* is a core member of the Paradisaeidae-Ptilonorhynchidae group, with its pattern lying between the normal patterns for paradisaeine and cnemophiline birds-of-paradise and reminiscent of that of bowerbirds; 3) *Platylophus* is not a corvid and *Podoces, Pseudopodoces*, and *Ptilostomus* are probably not, either; and 4) *Grallina* shows no pterylographic relationship to *Struthidea* and *Corcorax*.

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KEYWORDS: Atrichornithidae, Corvidae, Menuridae, Paradisaeidae, Ptilonorhynchidae, Grallinidae, Artamidae, Callaeidae, Cracticidae, Oriolidae, Dicruridae, Sturnidae, Laniidae, pterylosis, relationships.

Results of my initial study of the body pterylosis of the Passeriformes (Heimerdinger, 1964) strongly suggested that study of this character system in the 'corvid assemblage' could help to determine relationships therein. In contrast to many oscines, the crows and jays and some of the other groups commonly considered to be related to them, seemed to show distinctive features in their pterylosis—either dorsal or ventral or both. Since the initial study, I gradually have acquired a broad sample of specimens of most of the genera involved. As I reported at the XVIth International Ornithological Congress in Canberra (Clench, 1975, incorporated in the present study), I consider the Menurae to be related to this assemblage, and hence have delayed publication until an adequate specimen of *Atrichornis* was available to complete the series.

In the following report I have included descriptions and discussion of not only *Atrichornis* and *Menura* and those families often regarded as part of the corvid assemblage (Corvidae, Sturnidae, Paradisaeidae, Ptilonorhynchidae, Cracticidae, Artamidae, Grallinidae, Callaeidae, Dicruridae and Oriolidae), but also a few problem genera such as *Pseudopodoces* (discussed under Corvidae), *Prionops* (Laniidae), *Turnagra* (Paradisaeidae, *sensu lato*), *Picathartes* (Muscicapidae), *Pityriasis* (Laniidae), *Platylophus* (Corvidae) and *Ptilostomus* (Corvidae) which have been suggested to be allied to the corvid group (review in Amadon, 1944). I have also included brief remarks on two other groups: 1) the Furnarioidea, in light of the recent suggestion by Feduccia and Olson (1982) of the possible relationship of the Rhinocryptidae to the Menurae; and 2) the Vireonidae and a few other oscine groups, in response to Sibley and Ahlquist's findings (1982, in press) that the vireos are closely related to members of the corvid assemblage.

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METHODS AND TERMINOLOGY

In general, I have followed the flat-skin technique described previously (Clench, 1970), but have largely

omitted the X-ray step from the procedure and studied the undersurface of the skins directly under a binocular dissecting microscope. In a few instances (indicated in the text), I have used already-clipped, alcohol-preserved specimens or the interior of museum study skins when better material was not available. Many of the flat skins used were, of necessity, prepared from specimens in alcohol, and some from specimens that were in very poor condition (e.g., in heavy moult or rotting when preserved, badly shot-damaged, heavily dissected previously). In most instances, however, even the poorest specimens offered at least a general indication of the pterylosis pattern, and the feather rows in some parts of the tracts could be counted. The counting procedure and the discrimination of row patterning are the same as previously described (Clench, 1970). To avoid confusion in this paper, I have adopted the convention of using arabic numerals for the numbers of feathers in a row, and writing out the numbers of rows (e.g., 6 feathers in row six).

The problem of pterylographic terminology remains a knotty one. I follow the concept originated by the founder of pterylography, C. L. Nitzsch (1840, 1867): that a bird's body is feathered by a few large tracts. Each of these major tracts may be further subdivided as the smaller units are discernible and as appropriate for the species under study. Therein lies the most difficult terminology problem: a universally acceptable name for these smaller units. Various pterylographers (those writing in English) have called the subunits 'portions', 'branches', 'regions', 'areas' and 'elements' (Clench, 1970). The other school of thought, most recently expounded in detail by Lucas & Stettenheim (1972), regards each of these discernible units as a 'tract', with no term other than a collective, such as 'capital tracts', for the major divisions. Clearly there is a philosophical difference here that is difficult to resolve.

The International Committee on Avian Anatomical Nomenclature has compiled a comprehensive list of the anatomical structures of birds (Baumel *et al.*, 1979). The pterylosis terms were compiled primarily by A.M. Lucas (Baumel *et al.*, 1979) and follow the concept of many small tracts, although the number is somewhat reduced from that in Lucas & Stettenheim (1972). It is beneficial to standardize nomenclature but, like Homberger (1980), I am unable to accept certain terminology in the *Nomina Anatomica Avium*; my problem is with the basic premise that each small unit of feathers should be called a 'tract.' Accordingly, and in a compromise that should not be confusing, I have revised my terms to conform as far as possible to that of the International Committee (Table 1). My basic departures from the *Nomina* terminology are three: that each major body tract is a single unit, divided into parts (pars); that the 'Ptt. cervicales,' both dorsal and ventral, are properly regarded as parts of the capital tract (Clench, 1970); and that the ventral tract has only two divisions—pectoral and abdominal.

The taxonomy followed here is basically that of 'Peters' (Mayr & Greenway, 1960 and 1962; Traylor, 1979).

RESULTS

Atrichornis clamosus: Noisy Scrub-bird

The body pterylosis of *Atrichornis* is described here for the first time. It is perfectly passerine and perfectly oscine in its general patterning. Its exceptional aspects are not the tract patterns but the numbers of feathers contained in the tracts; this species is extremely densely feathered.

Pteryla Spinalis (Fig. 1). The entire tract, as is usual for a passerine, is composed of chevron-shaped rows, with the central feather of each row lying on the body midline. The anterior portion of the neck skin was not removed from the specimen so as to minimize damage for other studies, thus the length of the pars interscapularis was not determined (nor has this length ever proved to be a taxonomically important aspect of pterylography). Most of the central rows of the pars interscapularis contain 6 feathers on a side (counting the central feather), and the posteriormost three rows have 5 on a side. The pars dorsalis consists of twelve complete rows. They are 'complete' in that they all have a central feather and thus do not form a midline apterium. Two anterior rows, however, have a small gap in their lateral arms, a feature found in many birds and apparently an individual variant of little or no significance (e.g., the extra 'lateral row' in *Passer* and other oscines; Clench, 1970). The first row of the pars dorsalis contains 6 feathers, then a gap of 1 space, followed by 2 more feathers to complete the row, for a count of 9; the second row is entire with 10 feathers on a side; the third is also gapped, with a space of 2 between the 10th and last 2, thus is 14 feathers long; and the remaining rows are all entire, with (one side) counts of 15, 13, 11, 10, 9, 8, 7, 7, 7. The total number of feathers in the pars dorsalis is 228, and the shape is of a rounded rhombus. The pars pelvica consists of eleven rows with the following (one side) counts: 5, 5, 5, 5, 5, 6, 7, 6, 5, 3, 1. It is also very densely feathered for a passerine but otherwise has the normal

Clench (1970)	*Nomina Anatomica Avium*	This Paper
Dorsal Tract	Pterylae Spinales	Pteryla Spinalis
—	Pt. cervicalis dorsalis	—
anterior element	Pt. interscapularis	pars interscapularis
saddle element	Pt. dorsalis	pars dorsalis
posterior element	Pt. pelvica	pars pelvica
Ventral Tract	Pterylae Ventrales	Pteryla Ventralis
—	Ptt. cervicales ventrales	—
flank element	Pt. pectoralis	pars pectoralis
main element	Pt. sternalis et abdominalis	pars abdominalis

Table 1. Pterylographic terms for the major body tracts.

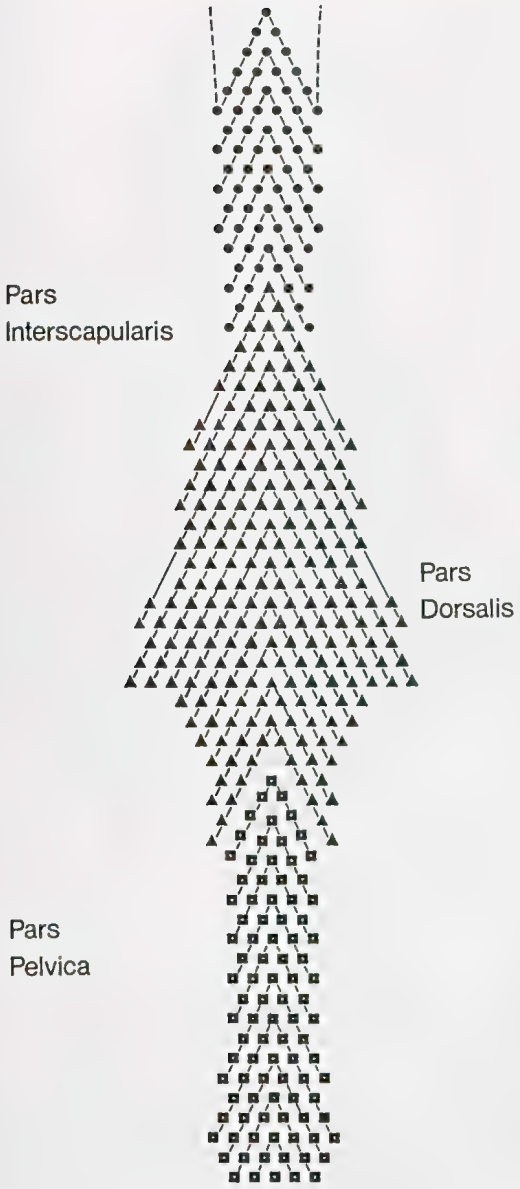

Fig. 1. *Atrichornis clamosus*, Pt. Spinalis.

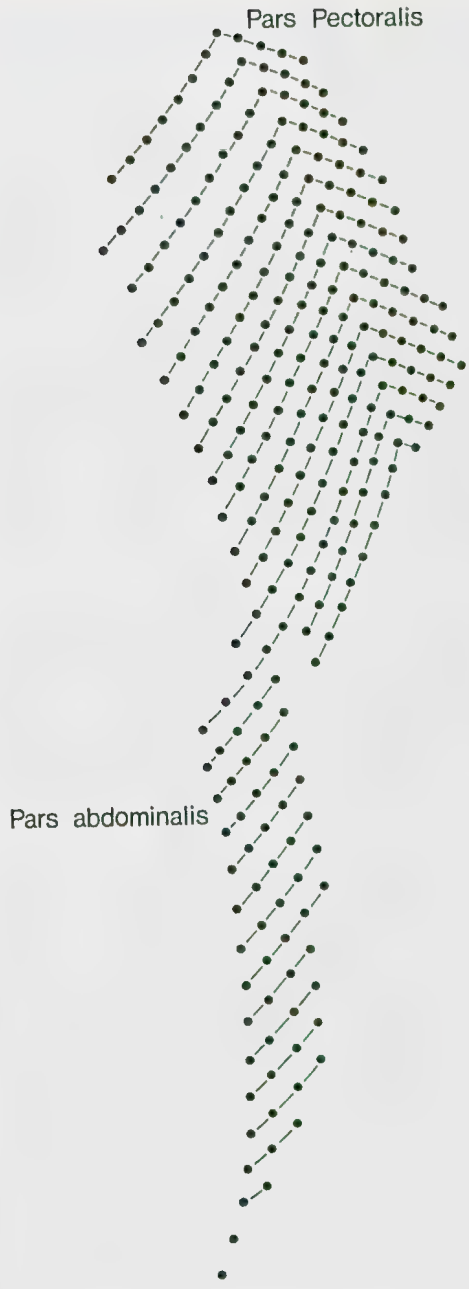

Fig. 2. *Atrichornis clamosus*, Pt. Ventralis.

configuration: straight-sided for the anteriormost half, then expands slightly before ending just anterior to the uropygial gland.

Although all the rows of the Pt. Spinalis are complete, with central feathers, the position of the first row of the pars pelvica relative to the last row of the pars dorsalis forms a small gap or false apterium at the base of the pars dorsalis. This gap is 1 mm wide and 3 mm long (in a formalin-preserved, slightly stretched, dried skin) and is formed by the central feather of the first row of the pars pelvica lying between the 4th feathers of the last row of the pars dorsalis, rather than between the 3rd feathers as it would if the spacing were even (Fig. 1).

Pteryla Ventralis (Fig. 2). This tract, like the spinal, is typically oscine in pattern but distinguished by exceptionally dense feathering. The lateral arms of the pars pectoralis contain 5 feathers (including the central) for the first eight rows; the next three rows contain 6 feathers per arm, and the pars then ends on the lateral side with counts of 5, 4, 3, 2—a total length of fifteen rows. The medial side of the pars pectoralis contains very long row arms, the first having 8 feathers, the next two having 10, and the next eight having 11. The twelfth medial row arm has 12 feathers, the thirteenth has 14, and the last two have 9. The pars abdominalis begins with seven single-armed rows with 5 feathers, then four rows of 4, one row of 3, one of 2, and two with a single

feather. The complete tract is twenty-eight rows long on each side.

The maximum width of the ventral tract (at row thirteen) is 17 feathers; the majority of the pars pectoralis rows contain 15 or 16. The separation of the pars pectoralis from the pars abdominalis is short, only two rows long.

Discussion. As noted in Clench & Smith (1985), I also studied a second specimen of *Atrichornis clamosus*, which was in poor condition. Accurate row counts cannot be made from this old specimen, but in all visible details it is the same as the newly collected one: the feathering is dense throughout; the pars dorsalis of the Pt. Spinalis is twelve rows long and contains well over 200 feathers; a 1 × 3 mm gap at the junction of the pars dorsalis and pars pelvica is clearly visible; the pars pelvica is eleven rows long; the pars pectoralis of the Pt. Ventralis is very wide, and its separation from the pars abdominalis is short—two rows.

Menura novaehollandiae: Superb Lyrebird

The dorsal body pterylosis of *Menura* is also typically passerine in patterning but is exceptionally densely feathered. Ventrally, however, *Menura* is almost unique within the Passeriformes in the length and type of separation between the pars pectoralis and pars abdominalis.

Pteryla Spinalis (Fig. 3). Even taking into consideration the large size of a lyrebird body, the pterylosis of this species can only be described as astonishing in its density of feathering. The pars interscapularis is comparatively weak and sparse anteriorly, but ends in very dense feathering as it joins the pars dorsalis. The pars dorsalis is long and heavy; eighteen rows form a rhombic configuration, with the following counts (one side): 25, 26, 24, 25, 26, 24, 23, 22, 20, 18, 17, 16, 15, 14, 12, 11, 10, 9. The total number of feathers (both sides) is 656. The pars pelvica is similarly heavy and long—approximately seventeen rows and straight-sided for most of its length. Unfortunately, in this specimen (CM Alc. Coll. no. 1834) the fat deposits and connective tissue over the rump feathering make it impossible to count all the feathers in the area.

A small gap at the base of the pars dorsalis is also largely obscured by fat deposits, so the point was verified on two study skins (AMNH 023975 and 554413) which were relaxed and opened. The first of these also seems to have a small gap at the anterior end of the pars pelvica; on the second specimen the gap is clear and is formed in the same manner as that in *Atrichornis*.

Pteryla Ventralis (Fig. 4). The lateral arms of the pars pectoralis contain 4 feathers from the first row to the tenth. The eleventh row has 5 feathers; the twelfth and thirteenth, 6; the fourteenth and fifteenth, 5; the sixteenth, 4; and the seventeenth, 2. The medial arm has 4 feathers in the first row, 5 in the second, and 6 in the third through fifth. The sixth through ninth rows have

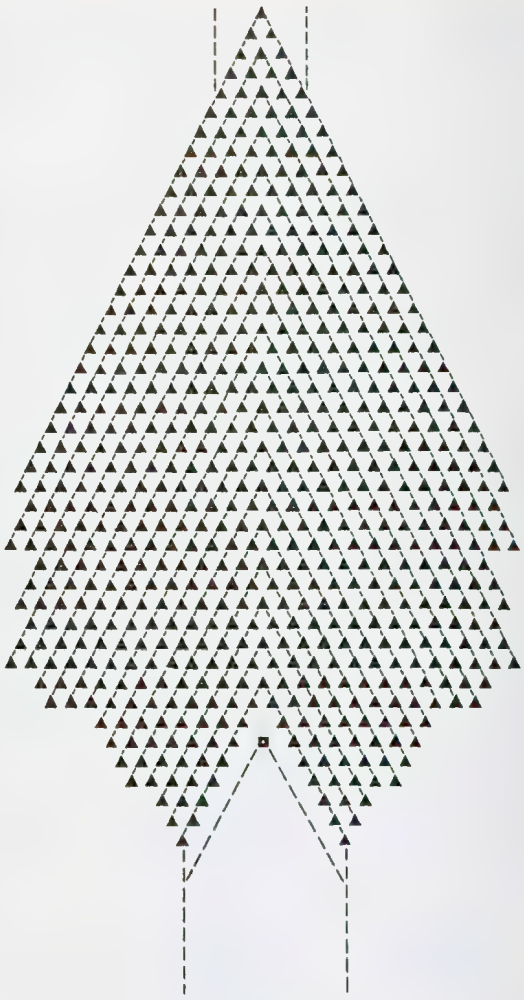

Fig. 3. *Menura novaehollandiae*, Pt. Spinalis, pars dorsalis.

7 feathers, but from the eighth through seventeenth the tract is too obscured by fat and connective tissue to provide accurate counts; the arms all contain either 7, 8 or 9 feathers until the seventeenth, which has 9.

The pars abdominalis does not begin as regularly spaced, additional feathers on the medial ends of the pars pectoralis arms as it does in other passerines (e.g., *Passer;* Clench, 1970). Instead, it first appears as a single, rather small feather opposite the end of row seven, but approximately 7 mm posteromedial to the end of that arm. The next rows (eight through fifteen) contain either 2 or 3 feathers (Fig. 4), and then the pars abdominalis becomes regular rows of 4 feathers (rows sixteen through thirty-four of the tract). The pars tapers and ends with rows of 3, 2, 1, 1, 1, 1 feathers. The total length of the tract is forty rows.

Discussion. Nitzsch (1867) figured the pterylosis of *Menura*, showing the very heavy Pt. Spinalis (but without the small gap at the base of the pars dorsalis) and the unusual configuration of the Pt. Ventralis. He commented that *Grallina* was the only other passerine he had examined with what he termed a 'half free' branch of the ventral tract.

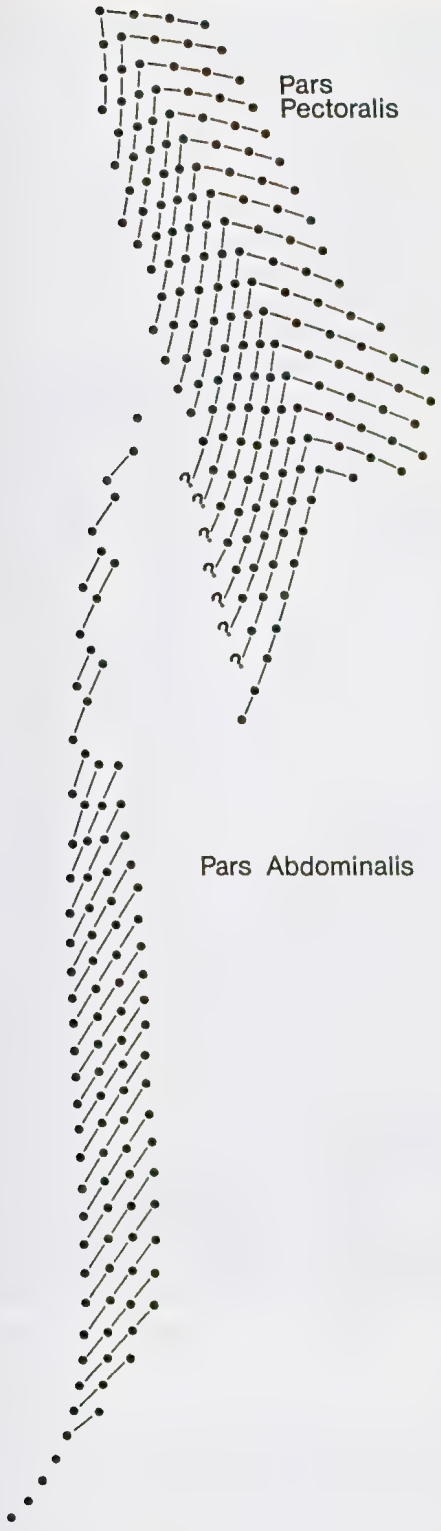

Fig. 4. *Menura novaehollandiae*, Pt. Ventralis.

I also confirmed the pattern and counts of the *Menura* flat skin with the two study skins. Fortunately, lyrebirds are large enough that the pterylosis pattern is relatively apparent in a study skin (in spite of the sawdust or other absorbent from the initial preparation that still adheres to, and may obscure, the calami and muscles of the tracts). I could see enough details, especially of the Pt. Ventralis, to confirm the counts from the alcohol specimen.

Paradisaeidae: Birds-of-Paradise

Previous studies. The initial pterylographic study of this family was by Nitzsch (1867), who reported on *Paradisaea apoda* (figured), *Ptiloris paradiseus* ('*Epimachus regius*') and *Epimachus fastuosus* ('*E. superbus*'). Giebel (1877) examined several additional species but used study skins for material; his work was strongly criticized by Pycraft (1905) and Stonor (1938) for its inaccuracy, and I concur. It will not be considered further. Pycraft (1905) studied *Paradisaea minor* (figured) and had *P. apoda, Manucodia comrii* and *Ptiloris paradiseus* for comparative material. Stonor (1938) conducted the landmark study of the family, examining 13 of the 20 genera ('Peters' classification) from spirit-preserved material, and 5 from study skins, internally examined. The only genera he was unable to obtain were *Pteridophora* and *Cnemophilus* (the latter then considered to be a bowerbird; Stonor, 1937). Since Stonor's report, there has been only one addition to the pterylographic literature on this family—notes on *Paradisaea rubra* by Berger (1956).

Material examined. Cnemophilinae: *Loria loria* (2 specimens), *Loboparadisea sericea* and *Cnemophilus macgregorii* (2 specimens). Paradisaeinae: *Manucodia chalybatus, M. comrii* (2 specimens), *Phonygammus keraudrenii, Ptiloris paradiseus, Semioptera wallacei, Seleucidis melanoleuca, Paradigalla (carunculata) brevicauda, Epimachus meyeri* (2 specimens), *Astrapia splendidissima, A. stephaniae, Lophorina superba, Parotia lawesii, Pteridophora alberti, Cicinnurus regius, Diphyllodes magnificus* (2 specimens), *Paradisaea apoda, P. raggiana* and *P. rubra*. The present series lacks three genera of Paradisaeinae (*Macgregoria, Lycocorax* and *Drepanornis*), specimens of which could not be located. The above material came from the AMNH, BM(NH), BPBM, Busch Gardens (through G.E. Woolfenden), the Pittsburgh Conservatory-Aviary (through CM), and the NYZS.

The *Paradisaea rubra* and *Seleucidis melanoleuca* were fresh specimens; all others were in alcohol.

Cnemophilinae. Unfortunately, the condition of the specimens ranged from poor to very poor (these are rare taxa in alcohol collections), so it was impossible to count all the feathers and rows in all individual specimens. The following is a conservative appraisal of the pterylosis of this subfamily.

The pterylosis of all three genera is similar. The Pteryla Spinalis is heavily feathered throughout, with a strong and wide pars interscapularis, and a pars dorsalis consisting of thirteen rows in *Loria*, at least eleven rows in *Loboparadisea*, and approximately thirteen in *Cnemophilus*. I could obtain relatively accurate counts of the pars dorsalis in both *Loria* specimens—254 and 225 feathers, respectively. The

main difference among the specimens is the presence or absence in the outermost row arms of from 1 to 4 feathers in the first and the ninth through thirteenth rows. The pars pelvica is similarly heavily feathered, with little or no expansion posteriorly. Clearly, there is no gap or apterium at the pars dorsalis/pars pectoralis junction. The Pt. Ventralis is unremarkable: there are approximately 9 feathers at the maximum width, the separation between the pars pectoralis and pars abdominalis is three or four rows long, and most of the rows of the pars abdominalis contain 4 feathers. The general configuration of these specimens agrees well with Stonor's figure of *Loria* (1938: 449).

Paradisaeinae. More of these specimens were in better condition, hence more specific counts could be made. As noted by Stonor (1938), species with extraordinary development of plumes on certain parts of the body have massive expansion of those portions of the pterylae. Fortunately, in no case do the plumes involve the pars dorsalis/pars pelvica, which is one of the most useful areas of body pterylosis for studying broad familial relationships. Because Stonor described and figured so many of these birds well, I shall simply add details to the material already published.

In strong contrast to the cnemophilines, the pars dorsalis of 'typical' birds-of-paradise is comparatively small and sparsely feathered. The number of rows ranges from seven to eleven. Unlike those of most oscines, the posteriormost rows of the pars dorsalis, and in some instances the feathers within those rows, are more widely spaced, presenting what Stonor termed a 'weakness' at the junction between the pars dorsalis and the pars pelvica. In addition, a small gap often occurs between the two—as in *Menura* and *Atrichornis* (e.g., *Semioptera wallacei*, Fig. 5). To a greater or lesser extent, this weakness and gapping are present in all specimens of paradisaeines examined. The possible exceptions are *Lophorina* and *Parotia* (poor specimens, but they do not seem to have a gap), and *Astrapia splendidissima* in which the central feather of the last row is absent, forming a small apterium (not true of the *A. stephaniae* specimen). The general strength of the pars dorsalis ranges from very sparsely and lightly feathered to moderate. In the specimens examined, the length of the pars dorsalis (number of rows) and its number of feathers are as follows: *Cicinnurus regius* 7/83; *Semioptera wallacei* 7/89; *Seleucidis melanoleuca* 7/97; *Paradigalla brevicauda* 7/?; *Phonygammus keraudrenii* 7/105; *Manucodia chalybatus* 8/92; *M. comrii* 8/116; *Lophorina superba* 8/119; *Diphyllodes magnificus* 8/102 and 8/128?; *Ptiloris paradiseus* 9/147; *Epimachus meyeri* 10/172 and 10/180; *Parotia lawesii* 10/142; *Pteridophora alberti* 10/150; *Paradisaea apoda* 10/144; *P. rubra* 9/155; *Astrapia splendidissima* 11/200; and *A. stephaniae* 11/201. As I have noted before (Clench, 1970), body size *per se* seems to have little to do with the number of feathers in the pars dorsalis; within closely related groups the basic patterns are the same. In paradisaeines, both large species

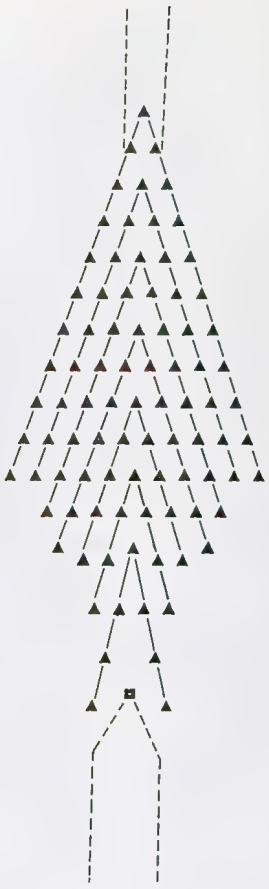

Fig. 5. *Semioptera wallacei*, Pt. Spinalis, pars dorsalis.

(*Seleucidis*) and small (*Cicinnurus*) have similar pterylae, and the most heavily feathered paradisaeines are the medium-sized *Astrapia* spp. *Astrapia* is also the only genus that approaches the cnemophilines in general strength of feathering, but it shows the weakness in the junction of the pars dorsalis/pars pelvica that is typical of paradisaeines.

The Pteryla Ventralis is considerably more variable than is the Pt. Spinalis, largely because of the species that have specialized flank plumes. As Stonor (1938) noted, and I have confirmed, sex apparently has no effect on the basic pterylosis: both males and females have the same pattern and degree of feathering, although the females do not have the long ornamental plumes.

The maximum width of the pars pectoralis ranges from 7 to 10 feathers in the species without specialized plumes (7 in *Phonygammus*, 8 in *Manucodia, Lophorina, Diphyllodes*, 9 in *Semioptera, Paradigalla* [?], *Pteridophora, Cincinnurus*, 10 in *Ptiloris*) and from 11 to approximately 28 in the flank-plumed birds (11–12 in *Epimachus*, 13–14 in *Astrapia*, 13 in *Seleucidis*, 18 in *Parotia*, approximately 25–28 in *Paradisaea*.) The separation between the pars pectoralis and the pars abdominalis ranges from three to seven rows long in most species; the longer separations are usually found

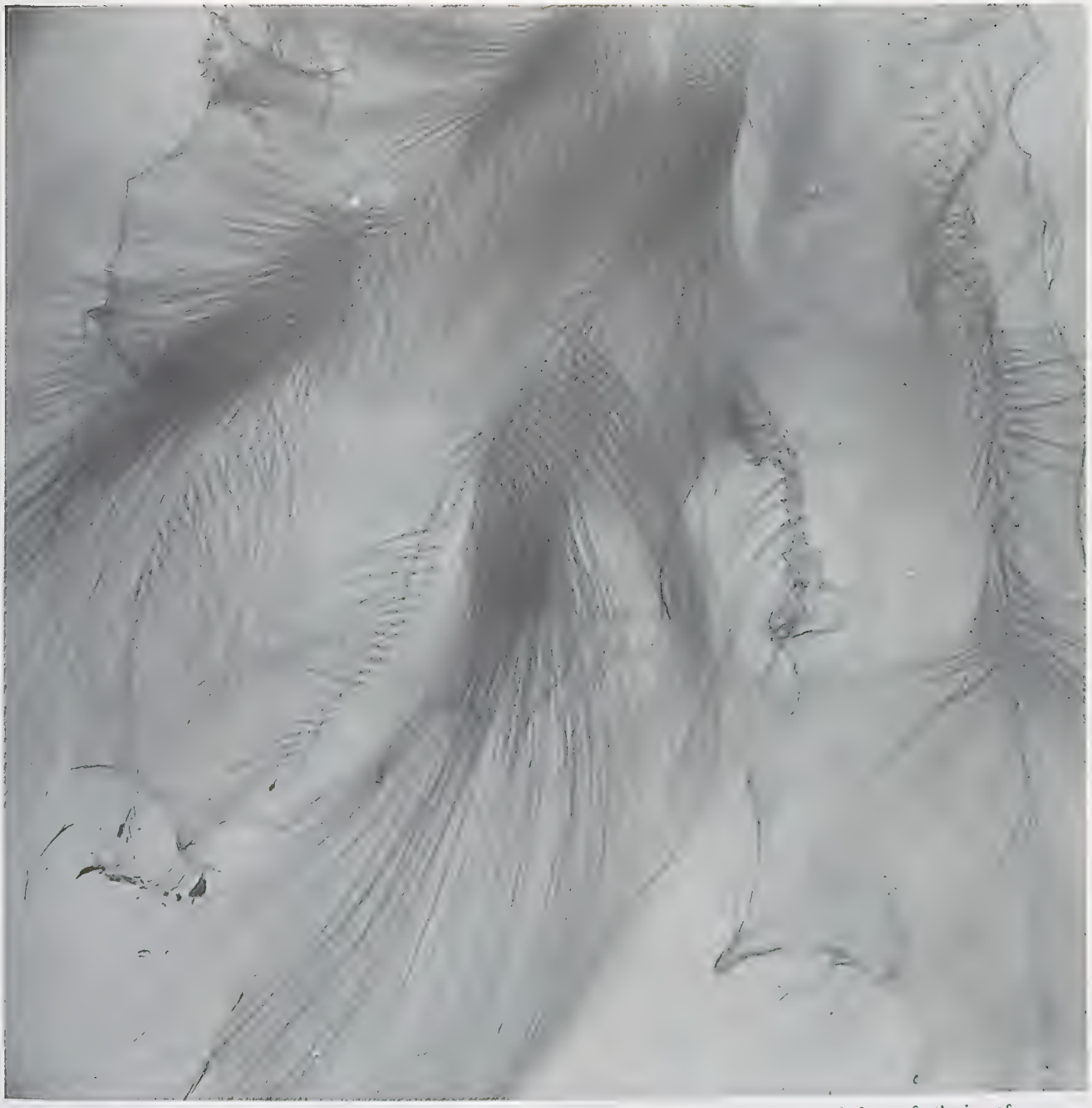

Fig. 6. *Seleucides melanoleuca*. Radiograph of flat skin. Pt. Ventralis on left, showing extremely heavy feathering of pars pectoralis; paired patches of heavy neck plumes (above) are components of Pt. Capitalis. Lightly feathered Pt. Spinalis on right.

in those forms with flank plumes. The exceptions are *Paradisaea* in which the massive development of the pars pectoralis extends into and partially obscures the separation of the pars abdominalis, and *Seleucidis* and several other genera which have a somewhat separated anterior end of the pars abdominalis, reminiscent of *Menura*.

In *Seleucidis* the first feather of the pars abdominalis is not as widely separated from the pars pectoralis as it is in *Menura*, but the general configuration is similar. The first few rows of the pars abdominalis also consist of 2, then 3, widely spaced feathers; the separated end of the pars pectoralis is long (approximately eleven rows) and heavily feathered (Fig. 6). The same configuration is apparent but less marked in *Epimachus, Cicinnurus* and possibly *Astrapia*.

In all the Paradisaeinae, the pars abdominalis is of normal passerine strength and configuration once it is separated from the pars pectoralis, and it is either 3 or 4 feathers wide through most of its length (5 in *Epimachus* and *Astrapia*).

Ptilonorhynchidae: Bowerbirds

Previous studies. Nitzsch (1867) examined

Ptilonorhynchus violaceus (*P. 'holosericeus'*) and *Sericulus chrysocephalus* (*S. 'regens'*) and found the body tracts to be narrow; the pars dorsalis of the Pt. Spinalis was described as rhombic with an elongated interior apterium. Pycraft (1905) studied the same two species, and his brief description agreed with that of Nitzsch. Stonor (1937) described and figured the pterylosis of *Amblyornis* in detail. (Note that the legends of Stonor's figures 6 and 8 were transposed in printing so that the illustration labeled *Semioptera wallacei* is actually *Amblyornis*.) Stonor found the Pt. Spinalis to have a broad rhombic pars dorsalis containing "a long and well-defined ellipsical apterion" (1937: 481). The Pt. Ventralis was typically passerine in configuration. He also described the pteryloses of *Ptilonorhynchus* and *Chlamydera* to be virtually identical to that of *Amblyornis*.

Material examined. *Ailuroedus crassirostris, Scenopoeetes dentirostris* (from the interior of a study skin only), *Amblyornis macgregoriae, Sericulus bakeri, S. chrysocephalus, Ptilonorhynchus violaceus* and *Chlamydera lauterbachi*. Specimens of *Archboldia* and *Prionodura*, the other genera in the family, could not be located. The specimens of *Ptilonorhynchus* and *Sericulus* were fresh (Pittsburgh Conservatory-Aviary through CM, and NYZS); the others were alcohol-preserved (AMNH).

Pteryla Spinalis. The pterylosis of all specimens studied is consistent in pattern: a strong, heavily feathered pars interscapularis, an equally strongly feathered pars dorsalis with a partial apterium, and a moderately strong to strong pars pelvica. The length of the pars dorsalis ranges from eleven rows in *Ailuroedus* and *Amblyornis*, thirteen or fourteen in *Sericulus* and fifteen in *Ptilonorhynchus*. The first rows are complete, with the feathers closely and evenly spaced; the posteriormost rows are incomplete, with the central (and sometimes the next-to-central) feathers absent and forming a midline apterium. In *Ailuroedus* the first six rows are complete and the last five have central feathers absent; the total feather count is 180. For *Scenopoeetes* I was able to examine only the interior of a study skin and could see that the tracts were similar to those of other bowerbirds (heavy pars dorsalis and a long apterium in the Pt. Spinalis), but feather counts were impossible. The *Amblyornis* is in poor condition but the first four rows of the pars dorsalis are clearly complete, the posteriormost seven are incomplete and the total feather count is approximately 228. The specimen of *Sericulus bakeri* is also in poor condition but probably has only four complete pars dorsalis rows and nine or ten incomplete. The *Sericulus chrysocephalus* was prepared from a fresh specimen, X-rayed, and later made into a study skin. It has seven complete rows anteriorly but the central feathers of rows five through seven have gaps to either side (Fig. 7), a not uncommon condition in species with apteria in the pars dorsalis. If these central feathers were not present, the configuration would be identical to that of the *S. bakeri* specimen. The total number of feathers in the *S. chrysocephalus* pars dorsalis is 235. The *Ptilonorhynchus* is also from a fresh specimen, and its pars dorsalis is shown diagrammatically in Figure 8. Rows one through five are complete, and six through fifteen are incomplete with a feather count of 281. The *Chlamydera* is badly shot-damaged and in moult, and affords little detail other than that the apterium is approximately six rows long in the pars dorsalis.

Pteryla Ventralis. This tract is typically oscine in all respects with nothing distinctive in the row patterning. The maximum width is either 10 or 11 feathers wide, the separation between the pars pectoralis and pars abdominalis is short (two to four rows long), and most of the rows in the pars abdominalis have 4 to 6 feathers.

Turnagra capensis: Piopio
(formerly 'New Zealand Thrush')

The only available alcohol material of this enigmatic New Zealand genus consists of two badly shot-damaged specimens in the BM(NH) and the Otago Museum. Nevertheless, the flat skins prepared from them give a general indication of the pterylosis, even if few feather counts are possible.

Pteryla Spinalis. Both the pars interscapularis and the pars pelvica are strongly feathered and unremarkable. The pars dorsalis, like that in the cnemophiline birds-of-paradise, scrub-birds and lyrebirds, contains extremely heavy feathering (approximately fifteen rows containing between 300 and 327 feathers in the two specimens). No small basal apterium or gapping is apparent but the condition of the specimens does not preclude the possibility of either.

Pteryla Ventralis. This tract is also heavily feathered, with a maximum width of 11 feathers, a separation between the pars pectoralis/pars abdominalis of four rows, and 4 to 5 feathers in most of the rows of the pars abdominalis.

Discussion. In a recent study (Olson *et al.*, 1983) I compared the pterylosis of *Turnagra* with that of other members of the 'corvid assemblage' and to various muscicapids with which a relationship has been suggested. *Turnagra* is clearly allied to the Paradisaeidae-Ptilonorhynchidae complex and is most similar to the cnemophiline birds-of-paradise.

Grallinidae: Mudnest Builders

The Australian birds that build mud nests have long been obscure in their relationships, both to one another and to other passerines (McEvey, 1976). They have been variously classified—ranging from separate families for each of the three genera (Mathews, 1930) to being scattered separately through the 'corvid assemblage' in other, larger families (e.g., Sharpe, 1877). In 1950, Amadon tentatively placed all three genera—*Grallina* (including *Pomareopsis*), *Struthidea* and *Corcorax*—

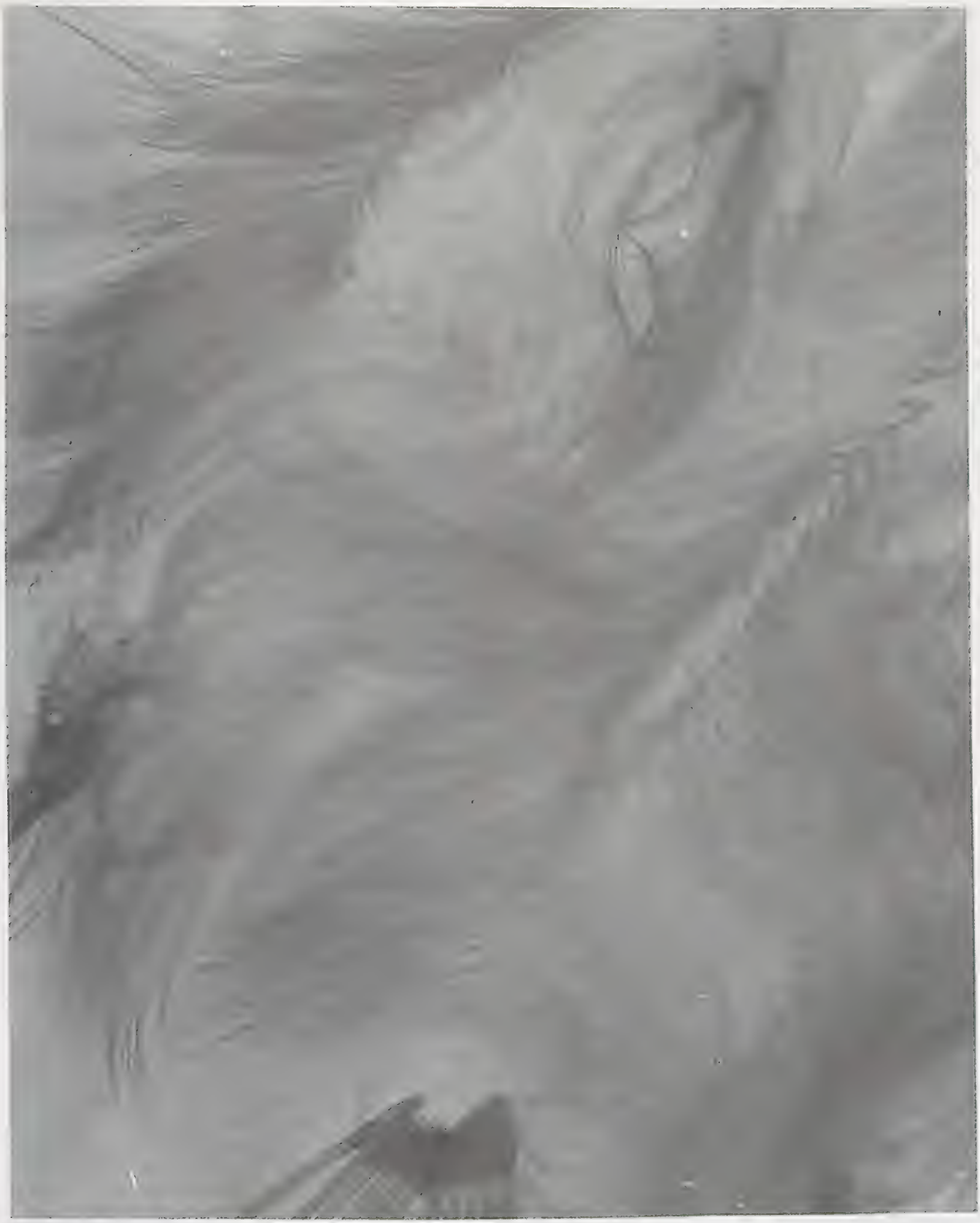

Fig. 7. *Sericulus chrysocephalus*. Radiograph of Pt. Spinalis, pars dorsalis. Anteriormost four rows complete; next three complete (with midline feathers) but well gapped; posteriormost six incomplete, forming an apterium.

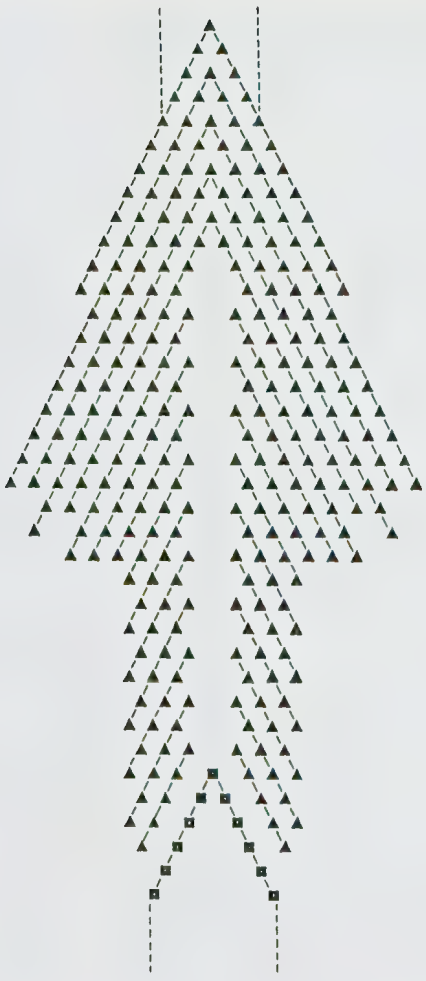

Fig. 8. *Ptilonorhynchus violaceus*, Pt. Spinalis, pars dorsalis. First five rows complete; last ten incomplete, forming an apterium.

together into the family Grallinidae, although he retained *Grallina* in a separate subfamily (Mayr & Amadon, 1951). This arrangement, which was "partly to avoid too many monotypic families" (Mayr & Amadon, 1951: 31), gained general acceptance (e.g., Mayr **in** Mayr & Greenway, 1962; Keast, 1964; CSIRO, 1969; Macdonald, 1973). It has usually been agreed that *Struthidea* and *Corcorax* are each other's closest relatives, and the main question has been the relationship of *Grallina* to them and to other passerines. Recently, Schodde (1975) separated them into two families—Grallinidae and Corcoracidae (including *Struthidea*)—but kept them adjacent to each other in his list. Slater (1974) retained *Grallina* in a monotypic family, but placed *Corcorax* and *Struthidea* in the Timaliidae. Chapman (1975) went even further, agreeing that *Corcorax* and *Struthidea* (but merged into a single genus) belonged in the babblers, and placed the Gralllininae as a subfamily of the Motacillidae.

As field observations and morphological information accumulate on these birds, their close relationship is becoming more in doubt; their habit of building mud nests (although of different shapes; Slater, 1974), their geographical distribution (endemic to Australia and New Guinea) and general similarities in skull structure (Amadon, 1950; but see also McEvey, 1976) seem to be about all they have in common. Sibley (1976) reported that egg white proteins of the three were extremely similar to one another but they were also similar to *Corvus* and paradisaeids, as well as generally similar to bowerbirds, *Oriolus, Menura*, cracticids, etc.—hardly a discriminating character in the degree of relationship at the family level. Recently, Sibley & Ahlquist (in press), after using a DNA-DNA hybridization technique, have included *Grallina* in the tribe of monarchine flycatchers, with the Corcoracinae well separated in another subfamily but both still in a huge superfamily 'Corvoidea.' The social structure of *Struthidea* and *Corcorax* is distinctly different from that of *Grallina* (Robinson, 1947; Rowley, 1974; Macdonald, 1973), the skeleton has important differences (Shufeldt, 1923; McEvey, 1976) and the appendicular musculature also shows certain dissimilarities (Borecky, 1977). The pterylosis also supports the conclusion that *Grallina* should be separated from the other mudnest builders.

Grallina. The only genus, of the three in question, that previously has been pterylographically studied is *Grallina*. Nitzsch (1867) described the Pt. Spinalis as having an undivided rhombic pars dorsalis and the Pt. Ventralis as sharing with *Menura* the otherwise unique type of separation of the pars abdominalis from the pars pectoralis. Clark (1945) found the same ventral configuration but disagreed on the shape of the Pt. Spinalis, pars dorsalis: "The dorsal tract is thickly feathered and conspicuous. In form it is intermediate between *Motacilla* [rhombic] and *Hirundo* [lobed] as figured by Nitzsch; that is, the outer angles of the anterior half of the tract are thickly feathered while the posterior half is abruptly narrow and the feathers are more widely spaced; indeed, there are but few feathers at the center of the area where widest. Removal of eight to ten feathers there would give a bilobed tract like that in *Hirundo*. These imperfect lobes are densely feathered but not sharply defined." (1945: 72) His text was accompanied by a sketchy diagram that showed the pars dorsalis as a broad triangle with no suggestion of the features mentioned. A similarly poor figure of *Grallina cyanoleuca* appeared in a report by Parsons (1968): the pars dorsalis was shown as a typically passerine rhombus, the pars pelvica was broadly expanded with an anchor-shaped pattern (heavier feathering?) within the element, and the Pt. Ventralis had an exceptionally broad pars abdominalis that separated from the pars pectoralis approximately halfway down the breast. Parsons stated, however, that the area between the pars dorsalis and the pars pelvica "gets very weak and would be discontinuous but for 5 or 6 small feathers" (1968: 42).

The single specimen of *Grallina cyanoleuca* (YPM alcoholic) available to me was moulting when collected and is in poor condition, which prevents a full count

of the tracts. The posteriormost pars dorsalis of the Pt. Spinalis has a moderately large and striking apterium. The entire element contains nine rows with the feathers of the first four evenly spaced; the fifth and sixth with central feathers slightly separated from the remainder of their rows; and the seventh through ninth clearly lacking a central feather and with a fairly wide space (3mm in a stretched flat skin) between the row arms. The pars pelvica is strong and twelve rows long but the specimen is too heavily in moult to confirm or refute the peculiar internal configuration indicated by Parsons (1968). The Pt. Ventralis is generally heavily feathered. The maximum width is 11 feathers and the pars pectoralis has a long, free segment (eight rows) posterior to its separation from the pars abdominalis. The latter separates from the pars pectoralis in the normal passerine manner—as a regular extension of the medial ends of the rows, not the essentially separate element as seen in *Menura*—but the separation is considerably more anteriad than is true of most other passerines. The majority of the pars abdominalis rows have 5 feathers.

Struthidea. My single specimen of *Struthidea cinerea* (BM(NH), alcohol-preserved) is also in moult, obscuring some details. The Pt. Spinalis pars dorsalis is nine rows long, with all rows complete (no apterium). The row counts (one side) are: 10, 10, 10, 9, 7, 6, 5, 4, 3, for a total (both sides) of 119 feathers. The midline feathers of the three or four posteriormost rows are slightly set apart but this gapping is so minor that it is visible only under the microscope. The pars pelvica is moderately strong with approximately eleven rows, and is broadly expanded posteriorly. The Pt. Ventralis is typically oscine in general configuration and strength: the maximum width is approximately 9 feathers, the separated pars pectoralis is five rows long and the pars abdominalis rows are 4 to 5 feathers wide.

Corcorax. Although I could not obtain a suitable specimen of this genus, I did examine one (BM 1925.11.1.149—specimen in alcohol, not skinned) in heavy molt. It was similar in all visible respects to the *Struthidea*, and clearly did not have a *Grallina*-like apterium in the pars dorsalis.

Discussion. *Grallina* differs from *Struthidea* in having an obvious apterium in the base of the pars dorsalis vs. a very slight gapping of the midline feathers in *Struthidea*. The pars pelvica of *Grallina* is also broader and more heavily feathered, especially posteriorly. Ventrally, *Grallina* differs strikingly in the length of the separated pars pectoralis (eight vs. five rows, or 17 mm vs. 9 mm in *Struthidea*).

In regard to the suggested relationship of *Grallina* with the Motacillidae, and *Struthidea/Corcorax* with the Timaliinae (Chapman, 1975), the pterylographic evidence argues strongly against the first and weakly against the second. Nitzsch (1867) and Verheyen (1953) figured *Motacilla, Anthus* and *Macronyx*, and I have examined a specimen of *Motacilla alba*: motacillids are typically oscine in all respects and show none of the striking peculiarities of *Grallina*. The babblers are a large and diverse group and have not yet been studied sufficiently. Those reports that do exist in the literature (Nitzsch, 1867: *Timalia, Pomatorhinus*; Shufeldt, 1889: *Chamaea*; Clark, 1914: *Garrulax*; Naik & Andrews, 1966: *Turdoides*) and my own preliminary examination of specimens (*Leiothrix lutea, L. argentauris, Stachyris pyrrhops*) indicate that the pattern in the pars dorsalis is uninterrupted, unlike the gapping seen in *Struthidea*. Much more material, however, will have to be examined before the relationship can be confirmed or denied by pterylography.

Artamidae: Wood Swallows

Previous studies. Nitzsch (1867: 80) described and figured *Artamus ('Ocypterus') leucorhynchus*. He stated that the pars dorsalis was elongated, rhombic and "narrow, but widened by the two powder-down tracts situated beside it", and that the pars pelvica was broad. The pars pectoralis was "somewhat separated" at its posterior end and had a band of powderdowns that extended from its posterolateral edge, dorsolaterally into the axillary region. The paired Pt. Femoralis on the base of the thigh similarly had a band of powderdowns on the medial side.

Lowe (1938a: 431) described *Artamus minor* to have "characteristic passerine pterylosis", with no mention of powderdowns. Parsons (1968) figured *Artamus cyanopterus ('tenebrosa')* with an elongated, lozenge-shaped pars dorsalis and a broad pars pelvica, without indication of powderdowns. His figure of the Pt. Ventralis, however, showed a lateral extension of the pars pectoralis that almost surely corresponds to the powderdown band illustrated by Nitzsch. Parsons did mention finding feathers with aftershafts in the Pt. Spinalis, mostly on the tract margins; apparently he did not recognize them as powderdowns.

Material examined. *Artamus leucorhynchus* and *A. insignis* (one each, CM and AMNH specimens in alcohol).

Pteryla Spinalis. The pars dorsalis of a wood swallow is remarkably modified. It is approximately eleven rows long, and a solid rhombus. The first 6 or 7 feathers in each row are normal contour feathers but at feather 7 or 8, to the end of the extended row, they are highly modified powderdown quills in sheath. The pars interscapularis and pars pelvica are generally strong; the latter is nine rows long in the specimen of *A. leucorhynchus* with (one side) counts of 6 feathers in the first six rows, then 4, 3, and 1 feather in the posteriormost.

Pteryla Ventralis. The tract is generally heavy, with a maximum width of 10 or 11 feathers in the pars pectoralis and 5 in the pars abdominalis. The separation of the pars abdominalis occurs at row nineteen and the pars pectoralis ends at row twenty-two; the tract as a whole is thirty-nine rows long. A broad band of powderdowns extends dorsolaterally from the posterolateral margin of the pars pectoralis (from near

the ends of rows seventeen to twenty-one) and reaches about halfway to the pars dorsalis on the back. Unlike the situation in the pars dorsalis, however, these powderdown follicles do not seem to be regular extensions of the ventral tract rows, but they are roughly organized and constitute a patch of about six rows of 16 feathers (maximum). There is a sparser and even less organized patch of powderdowns on the medial edge of the Pt. Femoralis and a few scattered powderdown follicles in the Pt. Cruralis.

Discussion. When viewed from the underside of the skin, the powderdowns in *Artamus* look like modified contour feathers. The follicles are essentially the same size as a (growing) normal *Artamus* contour feather, and they are either components of the regular body tracts or apparent developments of plumulaceous apterial feathers or ephemeral tracts (e.g., the 'axillary tract'; see comments in Clench, 1970). If one of these artamid powderdowns is plucked and examined, it is a good match to the illustrations of pigeon powder feathers in Lucas & Stettenheim (1972: 337). The same is true of the powderdowns in certain cotingids, although cotinga powderdown follicles tend to be larger than are the adjacent contour feathers (e.g., in *Conioptilon*) and they are very differently arranged on the body (see my comments in Lowery & O'Neill, 1966). In gross morphology, the powderdown patches of herons are even more strikingly different when viewed from the underside of the skin. Heron powderdown follicles are many times smaller than the nearby contour feathers (or than passerine powderdowns); they look like bits of fine thread, and appear to grow randomly in a flat mass of tiny follicles.

Callaeidae: New Zealand Wattlebirds

Previous studies. Nitzsch (1867) found *Callaeas* (*'Glaucopis'*) *cinerea* to have the same pterylosis as that of *Corvus*: a broad, acutely angled, rhombic pars dorsalis with an elongated apterium. Garrod (1872: 644) studied *Heteralocha acutirostris* (*'gouldi'*) and stated that "the arrangement of the feathers is completely passerine [the Huia's affinities had been suspected to be with the nonpasserine *Upupa*]. The rhombic saddle of the spinal tract does not enclose any ephippial space, therein differing from the Crow's and resembling the typical Starling's." Stonor (1942) studied all three genera in the family (*Callaeas cinerea, Heteralocha acutirostris*, and *Creadion* (*'Philesturnus'*) *carunculatus*) and found them to be essentially identical in body pterylosis. His description and figure of *Callaeas* showed the Pt. Spinalis to have a strong pars interscapularis and a broad, rounded, rhombic pars dorsalis without an apterium (contradicting Nitzsch but agreeing with Garrod) and without weakening in its posteriormost rows. The pars pelvica was broad and widened slightly to a triangular base just anterior to the uropygial gland. The Pt. Ventralis was characterized as follows (Stonor, 1942: 4): "The separation of the outer and inner tracts on the breast, as occurs in all Passerine birds, is but faintly indicated by a narrow 'notch' on the lower breast." He found all three genera to have unremarkably oscine pterylosis, differing among one another only by minor features of the capital tracts.

Material examined. Through the courtesy of J.D. Macdonald, I was given permission to remove the body skin from two BM(NH) spirit specimens: the long-extinct *Heteralocha acutirostris* (BM Reg. no. 1940.12.8.107) and the rare *Callaeas cinerea* (1940.12.8.109). The former had been collected in 1894, may have been originally preserved in rum (judging from its pungent odour), and was in heavy moult; it was in remarkably good condition for its museum age and stage of moult when collected. The *Callaeas* was collected at about the same time (data illegible — 1896?) and in excellent condition.

Pteryla Spinalis. In *Heteralocha* and *Callaeas* the pars interscapularis is broad and strong; its posteriormost row has 6 feathers per arm. The pars dorsalis in both genera is fourteen rows long and contains 298 feathers. The rhombic shape of the pars dorsalis in *Heteralocha* is slightly wider and more flared posteriorly than in *Callaeas*, which is a result of minor differences in the row arm lengths (11,18,18,18, 17, 15, 12, 11, 9, 8, 7, 5, 4, 3 in *Heteralocha* vs. 18, 18, 17, 16, 14, 13, 11, 10, 9, 8, 6, 6, 5, 5 in *Callaeas*). The occurrence of an apterium or gap will be discussed. The pars pelvica is strong and slightly expanded at its posteriormost end as illustrated by Stonor (1942).

Pteryla Ventralis. Both *Heteralocha* and *Callaeas* have the same highly unusual configuration of this tract. Throughout, the feathering is extremely heavy and there is no separation of the pars pectoralis from the pars abdominalis in the flank area. The maximum width above the flank is 10 feathers per row, and the lateral row arms contain 4 feathers. The flank ends by a gradual shortening of the lateral arms but, aside from a few slight irregularities in feather placement where the separation normally occurs in passerines, no true break occurs between the two pars. The pars abdominalis below the flank is wide, 7 feathers in *Callaeas*, 6 (perhaps 7? — obscured by moult) in *Heteralocha*.

Discussion. The major difference between the two specimens lies in an apparent apterium in the posterior pars dorsalis of *Callaeas*. In that specimen the first six rows are normal with the feathers evenly spaced. At row seven there is a small gap between the midline and first arm feathers; at rows eight and nine the gap is slightly wider and the apparent apterium (visible macroscopically) begins. The midline feathers from row eight through fourteen become progressively smaller. At the last (fourteenth) row the feather is so small as to be almost invisibile under a microscope, and the gap of the 'apterium' is 4 to 5 mm wide across the centre of the pars. At row eleven the central feather is 3 mm from its nearest lateral neighbor (feather number 3 of row ten), compared with an average distance of 1 mm between the rest of the saddle feathers. In the

Heteralocha specimen no apterium is apparent, except for a suggestion of a gap on either side of the midline in the posteriormost rows. Unfortunately, the heavy stage of moult in this bird precludes detailed analysis.

This variation, an apparent apterium formed by gaps in the spacing between (progressively smaller) midline feathers and their corresponding row arms, is also found in other passerines such as corvids (q.v.). I suspect this phenomenon explains the discrepancies reported by Nitzsch vs. Garrod and Stonor. All three were careful workers, and I have seldom found cause to doubt their results. In answer to my query whether Stonor's specimen of *Callaeas* (registration number unknown) still existed in the BM(NH) spirit collection and was thus available for re-examination, P.J.K. Burton reported (in litt.) that the collection now contains no clipped specimens of *Callaeas* (Stonor normally clipped the feathers from birds he studied pterylographically). Stonor also carried out other dissections for his study, so I can only conclude that he did not return what was left of the specimen to the collection (although he often did return clipped specimens of other species). Dr Burton also examined several other spirit specimens of *Callaeas* for me, and he reports (in litt.) that they seem to have small apparent apteria in the posterior pars dorsalis, but without clipping or skinning the specimens, he cannot be sure. I suggest, therefore, that members of this family may have a weakening in the posterior midline of the pars dorsalis, which may not be apparent in preserved specimens unless skins can be stretched out slightly to improve visibility.

Stonor (1942: 4) also described a condition in the Pt. Ventralis of *Callaeas* that is different from my findings: "The separation of the outer and inner tracts on the breast, as occurs in all Passerine birds, is but faintly indicated by a narrow 'notch' on the lower breast." Without Stonor's specimen to re-examine, I can only guess that it showed even more pattern interruption at the usual flank separation area than does mine, but more material would have to be examined to prove the point. Because my specimen of *Heteralocha*, and another of *H. acutirostris*, BM(NH) Reg. no. 1940.12.8.158, which I was able to examine superficially while it was on loan to R.J. Raikow, both lacked a true separation of the two pars of the Pt. Ventralis, I believe this feature is characteristic of the family.

Cracticidae: Australian Magpies

Previous studies. Nitzsch (1867: 80) described *Strepera graculina* (? = *Barita strepera*), *Cracticus torquatus* (? = *Barita destructor*) and *C. cassicus* (? = *Barita varia*) as "saddle short, broadly rhombic, acutely angled." Degen (1903) noted *Gymnorhina tibicen* as having a typical passerine configuration and agreeing well with the cracticid species described by Nitzsch. Leach (1914) described the pterylosis of *Strepera graculina* and, although his illustration showed peculiar differences from the standard passerine pattern (e.g., the Pt. Femoralis merging with the pars pelvica of the Pt. Spinalis, and the Pt. Ventralis continuous with the Pt. Cruralis and the wing feathering), he did not comment on these anomalies, stating just (p. 34) that "*Strepera, Gymnorhina* and *Cracticus* agree closely in the feather tracts." Clark (1945) re-examined and figured *Strepera graculina* and also described *Cracticus nigrogularis*. He criticized Leach's figure and stated that the Pt. Spinalis was heavy but of standard passerine configuration, that the connection between the pars pelvica and the Pt. Femoralis was "very incomplete", and that the Pt. Ventralis, especially the expansion of the pars pectoralis, was strong and similar to the pattern of *Paradisaea* in Nitzsch's illustration. Clark described *Cracticus nigrogularis* as being like *Strepera* but with a narrower, less densely feathered Pt. Ventralis. Parsons (1968) figured the dorsal pteryloses of *Gymnorhina (tibicen) leuconota* and *Strepera versicolor (intermedia)*, and both dorsal and ventral tracts of *Cracticus torquatus* (*'destructor'*). All three were shown with essentially similar pteryloses, the pars dorsalis being slightly narrower in *Cracticus*, broader and more rounded in *Gymnorhina*, and more angled in *Strepera*. *Cracticus* was figured with heavy ventral feathering in the pars pectoralis (except on its medial margin) and light feathering in the pars abdominalis.

Material examined. *Strepera graculina, Cracticus nigrogularis* (1 each, BM(NH) alcohol-preserved) and *C. torquatus* (YPM alcohol-preserved).

Pteryla Spinalis. The pterylosis of the three specimens is generally similar with relatively heavy feathering throughout, and the pars dorsalis in a rounded rhombic configuration. The pars dorsalis of *Cracticus nigrogularis* has 201 feathers in ten rows, with counts of 15, 16, 14, 12, 11, 10, 8, 7, 6, and (–)6. The posteriormost two rows show some gapping at the midline and the last row lacks a central feather, thus forming a small apterium. The specimen of *C. torquatus* is in poor condition (heavy moult) and cannot be fully counted, but the posterior end of the pars dorsalis (ten rows) shows similar gapping, with the last row clearly complete, although the midline feather is small.

Strepera graculina has a pars dorsalis of 198 feathers in eleven complete rows, with less posterior gapping but with the 1st midline feather of the pars pelvica lying between the 4th feathers (rather than the usual 3rd) of the last pars dorsalis row and hence forming a small space.

The pars pelvica is strongly feathered (84 feathers in ten rows in *C. nigrogularis*) and of the usual passerine configuration. In the *Strepera graculina* specimen, however, a few weak feathers lead off from the posteriormost rows and suggest the 'very incomplete' connection between the pars pelvica and the Pt. Femoralis reported for this species by Clark (1945) and Leach (1914) but not by Nitzsch (1867) or Parsons (1968). I consider that these small feathers are individual anomalies and have seen similar situations in a number of unrelated birds (e.g., *Pycnonotus leucogenys*;

Heimerdinger, 1964).

Pteryla Ventralis. This tract is similarly strong and of typical oscine configuration. The flank separation is clear and relatively long (five rows in all three specimens) but not as extreme as that in *Paradisaea* (*contra* Clark 1945). The maximum width of the pars pectoralis is 10 or 11 feathers and the pars abdominalis is predominantly 5 feathers wide.

Discussion. The pterylosis of this family seems to be relatively uniform with strong feathering throughout the body tracts. The only noteworthy variation lies in the extent of the midline gapping and presence or absence of a small apterium in the posteriormost rows of the pars dorsalis.

Oriolidae: Old World Orioles

Previous studies. Nitzsch (1867) figured *Oriolus oriolus* ('*galbula*' [sic]) with a typical passerine pterylosis except that the pars dorsalis was lanceolate rather than rhombic in configuration, and the pars pectoralis was not separated from the pars abdominalis. Verheyen (1953) figured *Oriolus auratus (notatus)* with a similar shape dorsally and a complete lack of differentiation ventrally. Urik (1983) studied *Oriolus chinensis, O. auratus, O. oriolus* and *Sphecotheres flaviventris*; his findings of a lanceolate pars dorsalis with ten (*Sphecotheres*) to twelve (*Oriolus*) rows and the details of the Pt. Ventralis are essentially similar to mine (this study).

Material examined. Two fresh specimens of *Oriolus trailli* (♀ and ♂ from the NYZS).

Pteryla Spinalis. The tract is heavily feathered throughout with the pars dorsalis long and lanceolate in shape. The pars dorsalis is composed of 234 feathers in twelve rows (16, 16, 15, 14, 13, 11, 9, 7, 7, 6, 5, 4) in the female specimen; the male (in moult) seems to be identical. The pars pelvica is eight rows long and of the usual oscine configuration.

Pteryla Ventralis. The total length is forty-one rows. The first row is a chevron of 6 feathers and the maximum width of 9 is reached at row ten. The pars pectoralis separates at row twenty-two and ends at twenty-six. The pars abdominalis posterior to the separation has 6 feathers per row for most of its length. Both specimens are identical.

Discussion. The heavy feathering of the Pt. Ventralis may have caused Nitzsch to miss the separation of the pars pectoralis from the pars abdominalis—as apparently has been the case with many pterylographers in many instances. Verheyen's figure of the Pt. Ventralis is so generalized as to be completely misleading.

Dicruridae: Drongos

Previous studies. Nitzsch (1867) described *Dicrurus macrocercus* (*'Edolius bilobus'*) as having a very small apterium at the base of the rhombic pars dorsalis and a broad Pt. Ventralis with a slight separation of the pars pectoralis and pars abdominalis. McDowell (1947: 303) published a short description of *Dicrurus adsimilis* (*'modestus'*) based on the examination of an unclipped specimen in alcohol (AMNH). Accuracy is impossible using his method, so until the same species (perhaps the same specimen) can be re-examined, I put little reliance on McDowell's description of a pars dorsalis without an apterium, one side of the posterior Pt. Ventralis "uniting with its fellow to surround the cloaca", and other anomalies. Urik (1983) examined *Dicrurus macrocercus, D. hottentottus* and *Chaetorhynchus papuensis*. Both *Dicrurus* specimens had wide gapping or a true apterium in the posterior pars dorsalis, and a pars dorsalis that was nine rows long; both tracts were similar to my findings. *Chaetorhynchus* differed dorsally by lacking an apterium and by having a posteriorly expanded pars pelvica.

Material examined. A fresh specimen of *Dicrurus paradiseus* (NYZS) but in heavy moult.

Pteryla Spinalis. The pars interscapularis is moderately broad, with most of its rows having 5 feathers per arm. The pars dorsalis is long, narrow and lanceolate; an apterium is formed by the last two rows being incomplete on the midline. The pars dorsalis is approximately nine rows long (too many feathers lost to be certain). The pars pelvica is narrow and expanded at the base in the usual passerine configuration.

Pteryla Ventralis. The maximum width above the flank area is 8 feathers, the pars pectoralis separates approximately three rows before it ends at row twenty-one, and the entire length is about thirty-five rows (uncertainty the result of missing and growing feathers). The two horns of the pars abdominalis clearly do not meet or enclose the cloaca.

Laniidae: Shrikes

The shrikes are considered here because several genera that were long thought to be allied to starlings have been removed to the Laniidae and their allies (Amadon in Mayr & Greenway, 1962). Rand (in Mayr & Greenway, 1960) listed *Pityriasis* and *Prionops* within the Laniidae, and the vanga shrikes as a separate family; but Morony, Bock & Farrand (1975) consider *Vanga* and its relatives as a subfamily within shrikes, and thus they shall be treated here.

Previous studies. Nitzsch (1867) described several species of this family (both unspecified and specified, and including European *Lanius* spp. and *Prionops plumata*) as having a broad, uninterrupted, rhombic pars dorsalis that was "posteriorly abbreviated". Miller (1931) made a thorough study of *Lanius ludovicianus*. The Pt. Spinalis was described and figured with a heavy pars interscapularis; a broad, rhombic, almost fan-shaped pars dorsalis; and a pars pelvica ending in a triangular base. The Pt. Ventralis was shown to have a wide pars pectoralis with a single line of feathers

leading dorsally from its posterolateral margin almost to join the pars dorsalis. The pars abdominalis contained approximately 3 feathers per row and narrowed to a single line, meeting "its counterpart of the opposite side at a point just anterior to the anal circlet" (p. 129). Verheyen (1953) figured the Pt. Spinalis of four species: *Tchagra senegala, T. minuta, Laniarius ferrugineus* and *Telophorus nigrifrons*. All showed the same rhombic shape in the pars dorsalis and slightly triangular base in the pars pelvica, although the pars dorsalis of *Telophorus* was more oval than that of the others. Berger (1957: 237) studied the pterylosis of *Leptopterus ('Artamella') viridis*. He described the pars dorsalis as being diamond-shaped and similar to Nitzsch's figure of *Motacilla*. The pars pelvica was generally similar to Miller's figure of *Lanius*. Berger found the Pt. Ventralis to be wide anteriorly (the pars pectoralis) and two or three rows wide in the pars abdominalis. He also described "a discrete lateral thoracic tract (two to three rows wide), which extends dorsocephalad from the posterodorsal margin of the sternal tract [pars pectoralis] to the axilla". Dorst (1960) studied several species (unspecified) of vanga shrikes and wood shrikes, and described the former as having an uninterrupted, lozenge-shaped pars dorsalis and a narrow pars pelvica, and the latter as having a wider Pt. Spinalis. De Vree (1969) made a detailed study of *Tchagra minuta*. His figures are excellent and allow feather counts: the Pt. Spinalis is of typical passerine configuration, the pars dorsalis contains nine rows (7, 12, 11, 10, 9, 7, 6, 4, 3) with a total of 129 feathers, and the pars pelvica has seven rows with 27 feathers. The Pt. Ventralis is also of normal passerine shape, the maximum width of the pars pectoralis is 10 feathers, its length is about sixteen rows long and it separates from the pars abdominalis at row eleven. Most of the rows of the pars abdominalis are 4 or 5 feathers wide, and the entire tract is thirty-one rows long. De Vree used eleven specimens of *Tchagra minuta* for his study and found in only one a weak axillary tract of four or five small downy feathers.

Material examined. One fresh specimen of *Lanius schach* (YPM), single alcoholic specimens of *Pityriasis gymnocephala* (FMNH), *Prionops retzii* (YPM) and *Leptopterus chabert* (YPM).

Pteryla Spinalis. These specimens have very similar pteryloses, both dorsally and ventrally, and are of the type common to most oscines. The pars interscapularis is moderately strong, the pars dorsalis is expanded into a solid rhombic configuration, and the pars pelvica is relatively narrow and weak. The specimen of *Lanius schach* is somewhat different in that it has 126 feathers in only eight rows in the pars dorsalis (vs. 129 feathers in nine rows in *Tchagra*, approximately nine rows in *Leptopterus*, and ten in *Prionops* and *Pityriasis*); the first six *Lanius* rows are closely arranged and the last two are more spaced out with a very small gap before the beginning of the pars pelvica.

Pteryla Ventralis. The maximum width is nine or ten rows, the separated portion of the pars pectoralis is three to five rows long, and the pars abdominalis is 4 or 5 feathers wide through most of its length.

Discussion. Whether *Pityriasis* and *Prionops* are appropriately included within the shrikes cannot be answered with pterylography, but certainly the two genera show no pterylographic relationship with the Corvidae and allies (see below) and agree well with the Laniidae (albeit also agreeing with the patterns in many other passerine families).

The several reports of 'axillary tracts' and of the two horns of the pars abdominalis meeting above the cloaca are almost surely due to individual variation (and freshness of the specimens examined) rather than to any important variation.

Sturnidae: Starlings

Previous studies. Nitzsch (1867) found the Pt. Spinalis of starlings to be variable. *Gracula religiosa, Lamprotornis* and perhaps *Sturnus ('Pastor') roseus* (his wording is unclear) had a solidly feathered, rhombic pars dorsalis, whereas that element contained a very small apterium in *Sturnus contra ('capensis')*, *Acridotheres ('Pastor') tristis* and *Buphagus africanus*. Lowe (1938b) described the pars dorsalis of *Sturnus vulgaris* as broad and rounded, lacking an apterium. Berger (1957) made a careful study of the pterylosis of *Fregilupus varius*. His descriptions and figures showed the expanded portion of the pars pectoralis to be unseparated from the pars abdominalis. The Pt. Spinalis also presented an unusual configuration: the pars dorsalis was narrow and lobed but continuous with the pars pelvica which, in turn, ended in a barely expanded and pointed shape. *Sturnus vulgaris* and *Aplonis tabuensis*, in contrast, had a rhombic pars dorsalis. Berger also described *Sturnus* to have an expanded pars pelvica posteriorly and a wide, separated pars pectoralis in the Pt. Ventralis.

Material examined. Alcohol-preserved specimens of *Aplonis opaca, Poeoptera lugubris* (nestling, not skinned), *Onychognathus morio, Lamprotornis chalybaeus, Neocichla gutturalis, Cosmopsarus unicolor* (2 specimens), *Saroglossa aurata, Acridotheres cristatellus, Mino dumontii, Scissirostrum dubium* and *Buphagus erythrorhynchus* (YPM, BM(NH), USNM, AMNH), and fresh specimens of *Lamprotornis purpureus, Cinnyricinclus sharpii, C. leucogaster, Spreo superbus, Creatophora cinerea* (2), *Sturnus malabaricus, S. vulgaris* (3), *S. contra, Leucopsar rothschildi* (2), *Ampeliceps coronatus, Sarcops calvus* and *Gracula religiosa* (2) (CM, NYZS). This sample of 29 specimens represents 23 species of 19 genera in the family; 7 genera were not located.

Pteryla Spinalis. Within this sample of starlings, several distinct patterns are apparent in the pars dorsalis. In *Mino, Ampeliceps, Sarcops* and *Gracula* the element is relatively short, narrow and sparsely feathered, ranging from 47 feathers in five rows in *Gracula* to 79

feathers in seven rows in *Sarcops*. The feathers of the anteriormost two or three rows are slightly more closely arranged than are those of the posterior rows, and the spacing between the posteriormost midline feathers and the first feathers of their respective row arms is wider. In *Ampeliceps* the central feathers of the last three rows (four through six) are absent, as is the central feather of the last (fifth) row in one specimen of *Gracula;* neither *Mino, Sarcops* nor the other specimen of *Gracula* has an apterium.

In the other genera studied, the pars dorsalis is longer, wider and more abundantly feathered, with seven (*Sturnus* only) to nine rows containing from 100 to 136 feathers. The anteriormost rows are closely and evenly spaced, and the posteriormost show a gap of variable width between the midline feathers and the remainder of their rows; the posterior rows are also fairly closely and evenly spaced relative to each other.

The midline gap is very slight (visible only under microscopic examination) and otherwise the element appears to be a solidly and evenly feathered rhombus in *Aplonis, Saroglossa, Scissirostrum* and *Buphagus.* The gap is somewhat wider in *Lamprotornis, Neocichla, Cosmopsarus* and *Acridotheres.* In *Cinnyricinclus, Spreo, Creatophora, Sturnus, Leucopsar* and probably *Poeoptera,* the gap is moderately wide and clearly visible macroscopically. (The uncertainty about *Poeoptera* results from my being able to examine only an unskinned nestling; it has either a moderately wide gap or an apterium.) In addition to the midline gapping, these last genera tend to have the posteriormost rows more widely spaced from each other; the general appearance suggests a lobed pars dorsalis (formed by the more densely arranged anteriormost rows), with sparser feathering connecting the 'lobes' to the pars pelvica. Figure 9 is a radiograph of an adult *Sturnus vulgaris* showing the midline gapping (not extreme in this individual) and row spacing. In other preparations, such as direct examination of the underside of the skin or the study of a clipped alcoholic specimen, this 'lobed' effect is more apparent.

The pars dorsalis of *Onychognathus,* with 99 feathers in eight rows, has a long apterium; only the first three rows are complete, the apterium is wide, and the anteriormost rows are only slightly more closely feathered than are the posteriormost. The general appearance, however, is not like that of the *Mino* group because of the denser feathering.

Within the entire sample of starlings, the pars pelvica is strong (heaviest in *Sturnus vulgaris*) and variable in the width of its posterior expansion, but generally unremarkable.

Pteryla Ventralis. The maximum width of the pars pectoralis ranges from 8 to 11 feathers, the separated portion is three to five rows long, and most of the pars abdominalis rows are 4 to 6 feathers long. There is comparatively good retention of the group of small feathers that extends laterally from the posterolateral margin of the pars pectoralis ('axillary tract') as well as the minute feathers that extend across the abdomen from the posteriormost row of the pars abdominalis (see remarks on both these features in Clench, 1970). I believe these feathers tend to be retained in starlings because of the generally tough nature of sturnid skin. In most birds these small feathers tend to 'slip' easily and are often lost in preparation.

Discussion. The Sturnidae show more variation in the Pt. Spinalis than does almost any other passerine family (Heimerdinger, 1964; Clench, ms.). Yet, in spite of the several variants seen, a common pattern emerges: the feathers in the anteriormost rows tend to be more closely arranged than those of the posteriormost. The degree of spacing can lead to different appearances, from an almost solidly feathered rhombus to a seemingly lobed element with only a few feathers connecting it to the pars pelvica. There is also a tendency for midline weakness, ranging from slight gapping between the central posterior midline feathers and their row arms, through a wide gapping, to an actual apterium in a few forms. Morphologically speaking, the patterns in the Sturnidae can be arranged into a continuum, illustrating the stages that might be expected when a group was losing (or acquiring) an apterium. Therefore, despite the gradations in this family, the common, though variable, features of closely arranged vs. more loosely arranged rows, anterior to posterior, and the posterior midline weakness, seem to argue that the starlings are a natural group.

The explanations for the contradictory reports in the literature lie, I believe, in both the variability in the family, and in the condition of study material and the method of examination. It has long been customary to clip the feathers of an alcoholic specimen and study the pterylosis from the stubs of the calami remaining in the follicles. Depending on how strongly the feather musculature contracted when the specimen was fixed, small spaces between or within tracts could either be obscured or be plainly visible. Nitzsch (1867) reported a very small apterium in the pars dorsalis of *Sturnus contra* but probably not in *S. roseus.* I studied three species of *Sturnus*, including *S. contra,* and found all essentially similar; none had apteria but all had enough row-spreading and midline gapping in the posterior pars dorsalis that the spacing might be mistaken for an apterium in one specimen and covered by bunched follicles in the next. Similarly, Nitzsch's report of small apteria in *Acridotheres trisis* and *Buphagus africanus* may have resulted from the condition of the specimen; my specimens of *A. cristatellus* and *B. erythrorhynchus* had no apteria. Berger's report (1957) of *Fregilupus* contained two strong anomalies—the lack of a separated pars pectoralis and a lobed pars dorsalis. The former may reflect strongly contracted muscles in that region, for I have found numerous such reports in passerines to be in error; the separation is almost always there if one stretches the skin slightly and looks for the characteristic row patterning in the flank. The lobed pars dorsalis may be an extreme development of the

Fig. 9. *Sturnus vulgaris*, Pt. Spinalis. Pars dorsalis shows starlings' characteristic wider spacing between posteriormost rows.

condition I described for the *Sturnus* group, or it may be the result of poor external condition of the sole available specimen. Berger stated: "Though the plumage was badly discolored and most of the remiges and rectrices were broken, the muscles were, surprisingly, in excellent condition" (1957: 231). Yet, because Berger described *Sturnus vulgaris* as essentially the same as I found it, the lobed pars dorsalis of *Fregilupus* may well be a further extreme of the 'lobing' tendency and not an artifact.

Corvidae: Crows, Jays and Allies

Previous studies. The pterylosis of the crows and jays and their allies probably has been studied more than that of any other single passerine family. All authors found the ventral pattern to be relatively constant (e.g., Morlion & Vanparijs, 1979), but the Pt. Spinalis, pars dorsalis, showed variation. In most species this element contained a large, posterior midline apterium, but in a few others the pars dorsalis was a solidly feathered rhombus. Three species, *Pica pica* (Lowe, 1938b; Bock, 1962), *Corvus albus* (Dekeyser & Derivot, 1958) and perhaps *Nucifraga columbiana* (Bock, 1962) were described as having a 'forked' pars dorsalis, but this was almost certainly the result of a large apterium merging into a weak anterior end of the pars pelvica. Tables 2 and 3 summarize earlier findings and the results of the present study.

Material examined. Alcoholic specimens of *Calocitta formosa, Cissa chinensis, Cissilopha beecheii, Cissilopha sanblasiana, Crypsirina temia, Cyanocorax yncas, Cyanolyca mirabilis, Cyanolyca nana, Cyanolyca pumilo, Cyanopica cyana, Dendrocitta vagabunda, Gymnorhinus cyanocephala, Nucifraga columbiana, Perisoreus canadensis, Platylophus galericulatus, Psilorhinus morio, Ptilostomus afer, Temnurus temnurus* and *Zavattariornis stresemanni* (AMNH, BM(NH), CM, MLZ, SDMNH, USNM, YPM), and fresh specimens of *Aphelocoma coerulescens* (5 specimens), *A. ultramarina, Cissa chinensis, Corvus brachyrhynchos* (2), *Corvus corax, Corvus ossifragus, Cyanocitta cristata* (3), *Cyanocorax affinis, Cyanocorax caeruleus, Pica nuttalli (2) and Urocissa erythrorhyncha* (CM, FSM, NYZS, YPM, K.C. Parkes). I also examined alcohol-preserved specimens, but could not prepare flat skins from *Platysmurus leucopterus, Podoces hendersoni, Pseudopodoces humilis* and *Pyrrhocorax pyrrhocorax* (BM (NH)). This sample of 42 specimens represents 34 species of 25 genera in the family; the remaining genus, *Garrulus,* was well described by Morlion & Vanparijs (1979).

Pteryla Spinalis. The Corvidae may be divided pterylographically into three groups:

1. The Crows, Old World Jays and Allies — *Platysmurus, Garrulus* (data from Morlion & Vanparijs, 1979), *Urocissa, Cissa, Cyanopica, Dendrocitta, Crypsirina, Temnurus, Pica, Zavattariornis, Nucifraga, Pyrrhocorax* and *Corvus* (Fig. 10) — are characterized by having a strong pars interscapularis, a pars dorsalis with a long and wide apterium, and a moderately well

Species	Apterium Present	Apterium Absent	Reference[1]
Platylophus galericulatus[2]		×	1, 13
Platysmurus leucopterus	×		1, 13
Gymnorhinus cyanocephala	×		7, 13
Cyanocitta cristata	×	×	2, 9, 13 (see text)
Cyanocitta stelleri		×	4 (sp.?), 7
Aphelocoma coerulescens	×	×	4, 7, 9, 13 (see text)
Aphelocoma ultramarina		×	4, 13
Aphelocoma unicolor		×	4
Cyanolyca pumilo	×		13
Cyanolyca nana	×		13
Cyanolyca mirabilis	×		13
Cissilopha sanblasiana	×		13
Cissilopha beecheii	×	×	7, 13 (see text)
Cyanocorax caeruleus[3]	×		1, 13
Cyanocorax affinis	×		13
Cyanocorax chrysops	×		7
Cyanocorax yncas	×	×	7, 13 (see text)
Psilorhinus morio[4]	×		1, 7, 13
Calocitta formosa	×		7, 13
Garrulus glandarius	×		3, 7 (sp.?), 9, 12
Perisoreus canadensis		×	7, 9 (sp.?), 11, 13
Urocissa erythrorhyncha	×		13
Cissa chinensis	×		7, 13
Cissa thalassina		×?	1 (see text)
Cyanopica cyana	×		13
Dendrocitta vagabunda	×		1, 13
Crypsirina temia[5]	×		1, 13
Temnurus temnurus	×		13
Pica pica	×		1, 3, 7, 9, 12
Pica nuttalli	×		13
Zavattariornis stresemanni	×		13
Podoces hendersoni		×	13
Pseudopodoces humilis		×	13
Nucifraga columbiana	×		7, 9, 13
Nucifraga caryocatactes	×		9
Pyrrhocorax pyrrhocorax	×		13
Ptilostomus afer		×	13
Corvus monedula	×		12
Corvus frugilegus	×		3, 9, 12
Corvus brachyrhynchos	×		7, 13
Corvus ossifragus	×		13
Corvus corone	×		3, 9, 12
Corvus orru	×		10
Corvus coronoides	×		5
Corvus albus	×		8
Corvus corax	×		6, 7, 9, 13

Table 2. Pteryla Spinalis, pars dorsalis, of the Corvidae.

[1]References: 1. Nitzsch, 1867; 2. Peck, 1900; 3. Lowe, 1938b; 4. Pitelka, 1945; 5. Boehm, 1945; 6. Friant, 1948; 7. Mewaldt, 1958; 8. Dekeyser & Derivot, 1958; 9. Bock, 1962; 10. Parsons, 1968; 11. Ouellet, 1971; 12. Morlion & Vanparijs, 1979; 13. present study.
[2-5]'*Lanius scapulatus* Licht.', '*Corvus azureus*', '*Corvus fuliginosus*' and '*Glaucopis varians*,' respectively, of Nitzsch, 1867.

Genus	No. Rows	% True Apt.	% Apparent Apt.	No. Feathers	n[1]
Platylophus	6	0	0	50	1
Platysmurus	—	'long'	'long'	—	(1)
Gymnorhinus	10	50	50	c.139	1
Cyanocitta	10	0–30	20–30	157 [1][2]	3
Aphelocoma	10–11	0–30	27–40	157–178	6
Cyanolyca	10	20	20	c.162 [1]	3
Cissilopha	11	18–27	18–27	170–177	2
Cyanocorax	9–11	27–36	44–45	149 [1]	3
Psilorhinus	10	30	50	159	1
Calocitta	10	20	40	152	1
Perisoreus	13 (+?)	0	23	—	1
Urocissa	11	36	36	163	1
Cissa	10	30	50	163 [1]	2
Cyanopica	9	33	33	—	1
Dendrocitta	9	22	44	143	1
Crypsirina	10	40	40	c.130	1
Temnurus	9	33	33	122	1
Pica	9	33	44	147–156	2
Zavattariornis	9	33	33	114	1
Podoces	c.10	0	0	—	(1)
Pseudopodoces	c.9–10	0	0	—	(1)
Nucifraga	12	33	42	162	1
Pyrrhocorax	—	'long'	'long'	—	(1)
Ptilostomus	8	0	0	90	1
Corvus	11–12	55–67	55–67	110–198	4

Table 3. Pterylosis of the Corvidae: Pt. Spinalis, pars dorsalis.

[1]The specimens noted with parentheses were examined from unskinned alcoholic specimens and could not be counted completely.

[2]The numbers in square brackets denote the number in the sample that could be counted completely.

developed pars pelvica that ends in a triangularly expanded base. The length of the pars dorsalis ranges from nine to twelve rows (Table 3), and the apterium involves from two to eight (22% to 67%) of the posteriormost rows. The apterium is longest in *Corvus* and best developed in the species with the largest body size, *C. corax:* eight of the twelve rows (67%) lack central feathers in an otherwise strong element of 198 feathers. *Corvus ossifragus,* with a much smaller body size, has seven of eleven rows (64%) incomplete, with 110 feathers in the element; and the intermediate-sized *C. brachyrhynchos* (2 specimens) has six of eleven rows (55%) incomplete, with total feather counts of 155 and 165. In addition to the extent of the true apterium (midline feathers lacking), several of the genera have longer apparent apteria, caused by the posteriormost midline feathers being smaller than those more anterior, and by having wider spaces between them and the first feathers of the row arms — a 'gapping' mentioned previously. Thus, of this group, although *Dendrocitta* has the smallest apterium by percentage (two of nine rows, 22%), the midline feathers of rows six and seven are well gapped and the apterium appears longer than it actually is.

Nitzsch (1867) figured '*Kitta thalassina*' with a solidly rhombic pars dorsalis and with a line of feathers extending posteriad from either side of the pars. I have never seen a passerine with such a configuration and am sure that whatever Nitzsch's '*Kitta thalassina*' was, it was not *Cissa thalassina*. Both Mewaldt's (1958) and my specimens (3) of *Cissa (chinensis)* had large and obvious apteria. '*Kitta*' Temminck has erroneously been used in the past for *Cissa* (Blake & Vaurie in Mayr & Greenway, 1962). Nitzsch did not include *'Kitta thalassina'* in his group of 'Corvinae', but instead placed it in his 'Paradisidae' [sic], a grouping of birds-of-paradise and starlings. *'Kitta'* is also a synonym for *Ptilonorhynchus,* but that bowerbird has a large apterium in the pars dorsalis—as Nitzsch correctly reported. It is unfortunate that the system of terminology common in Germany during Nitzsch's period of activity (the first third of the Nineteenth Century) has largely fallen into disuse; it is now difficult or impossible to trace to modern taxa all the names he used.

2. THE NEW WORLD JAYS — *Gymnorhinus, Cyanocitta, Aphelocoma, Cyanolyca, Cissilopha, Cyanocorax, Psilorhinus* and *Calocitta*—have a strong pars interscapularis, a pars dorsalis of nine to eleven rows with a variably long-to-absent apterium, and a weakly to moderately developed pars pelvica that ends in a triangular base. *Gymnorhinus* has the best developed apterium (50% of its ten rows) and, along with *Psilorhinus* and *Calocitta,* has never been found to lack an apterium. The other genera of New World jays (with the possible exception of *Cyanolyca*) seem to be variable in this regard. Of my series of five *Aphelocoma coerulescens* (four from California, one a cage bird of unknown origin), one of the California birds lacks an apterium. My single *A. ultramarina* also lacks an apterium, as does one of three *Cyanocitta cristata.* Judging from the current results and from those of earlier studies (see Table 2), I believe that these New World jays may be in the process of losing (or gaining) the midline apterium. However, in all my specimens that have all the midline feathers present, and thus lack a true apterium, the birds show a semblance of an apterium by having the last rows gapped away from the midline feathers. In addition, the specimens with true apteria often have a longer apparent apterium by similar gapping (see Fig. 11 and Table 3).

3. ATYPICAL JAYS — *Platylophus, Perisoreus, Podoces, Pseudopodoces* and *Ptilostomus.* This assemblage of Old World or Holarctic jays falls together here only because, like most oscines, these genera have no apterium in the pars dorsalis; no particular relationship is implied. *Platylophus* strongly differs from any other corvid by its very short (six rows) and sparsely feathered (50) pars dorsalis. *Ptilostomus* has a relatively short (eight rows), lightly feathered (90) pars dorsalis, whereas *Perisoreus* lies at the other end of the scale with the longest (thirteen or fourteen rows) pars dorsalis, and one that is very densely feathered (not countable in my specimen). The base of the element in *Perisoreus* clearly has all the midline feathers present, but the posteriormost two to four rows are gapped, which gives the appearance of an apterium. The specimens of *Podoces* and *Pseudopodoces* were very unsatisfactory material (whole, alcohol-preserved

Fig. 10. *Corvus brachyrhynchos*, Pt. Spinalis.

Fig. 11. *Cyanocitta cristata*, Pt. Spinalis. Specimen has lost some feathers from lower right area of pars dorsalis but empty follicles are visible.

specimens, not flat skins), and I can state only that neither has an apterium in the pars dorsalis which is about nine or ten rows long.

Pteryla Ventralis. With exception of *Platylophus,* the ventral tract in this sample is unremarkable (Fig. 12). The maximum width of the pars pectoralis ranges from 8 to 11 feathers (12 in *Pica*), the separated portion is from three to five or six rows long (eight in *Pica*), and the pars abdominalis rows are primarily 3 to 5 feathers long. *Platylophus* is more lightly feathered, with a maximum width of the pars pectoralis of 7 feathers, the separated portion four rows long, and most of the abdominal rows having 3 feathers.

Discussion. In general, the Corvidae are characterized by having a relatively well developed apterium in the pars dorsalis. The New World jays differ somewhat by having a less developed apterium and sometimes none at all, although gapping in the posteriormost part of the element suggests a tendency toward an apterium. *Perisoreus* probably fits perfectly well into the New World jay group because it has the gapping, although it is generally more heavily feathered. However, birds that live in colder climates often have more feathers than do their tropical relatives (Clench, 1970); that tendency could be acting in the gray jays.

Goodwin (1976), Amadon (pers. comm.) and others have suggested that *Platylophus* may not be appropriately placed in the Corvidae. The pterylographic evidence indicates that the Crested Jay is not a corvid, although its generalized oscine pattern (a solidly feathered, rhombic pars dorsalis) is of little help in the search for its true affinities. Borecky (1977) found *Platylophus* to be perfectly corvid in its limb musculature. In contrast, Borecky (1978) reported that the musculature and other traits of *Pseudopodoces* were very uncorvid and suggested that *Pseudopodoces,* but not *Podoces,* be removed from the family. Borecky and I used the same specimens of both genera. Again, the pterylosis patterns of *Pseudopodoces* and *Podoces* are of little assistance in answering the question because they are of the generalized oscine type. *Zavattariornis,* on the other hand, fits well pterylographically into the Corvidae, although its position in that family has been questioned by Goodwin (1976) and others.

Ptilostomus does not seem to be a corvid. I have not seen any recent suggestions to the contrary, aside from Goodwin's (1976) uncertain placement of the genus at the base of the corvid family tree, with *Zavattariornis* possibly branching off from *Ptilostomus* (the latter suggestion not borne out by the pterylosis). Unfortunately, the pars dorsalis of *Ptilostomus* is of the generalized passerine type, so it is of little assistance other than to support the argument against a relationship with the crows and jays. Judging from the behavior, zoogeography and other published information on the Piapiac, I would be inclined to consider the Sturnidae (near *Buphagus?*) as the most fruitful area to look for relationships, but *Ptilostomus* would also be a fairly aberrant starling; the general strength of the pterylosis fits that of starlings, but the single specimen I was able to locate had no suggestion of the pars dorsalis basal gapping so characteristic of (but not universal in) the Sturnidae. The specimen was very old, alcohol-preserved and in moult at the base of the pars dorsalis, so the pattern was not clear. Better material might answer the question.

Furnarioidea: Woodhewers, Ovenbirds, Antbirds and Tapaculos

Feduccia & Olson (1982) have found a strong similarity between the Menurae and the Rhinocryptidae. The Rhinocryptidae, as well as other families in the Furnarioidea, have a complex array of pterylosis patterns (Clench, ms.), and a discussion of them is beyond the scope of this paper. However, in my current series of 133 flat skins representing 92 species of 73 genera in this superfamily (including 8 of 11 genera of Rhinocryptidae and 37 of 53 Formicariidae), no specimen shows the unusual configuration of the Pt. Ventralis seen in *Menura* and some Paradisaeidae. I have not counted the feathers in the entire series, but preliminary study also indicates that no furnarioidean has the density of ventral feathering as that in *Atrichornis* and *Menura.* A few have superficially similar Ptt. Spinales, notably *Chamaeza* (but not other formicariids) and some, but not all, rhinocryptids. Until I have the opportunity to report on my series of New World suboscines in detail, I can only state that pterylography only mildly suggests a relationship between the Menurae and the Furnarioidea.

Muscicapidae, Vireonidae and other Oscines

The problematical African genus *Picathartes* has been known pterylographically for many years (Lowe, 1938b) but, unfortunately, that information has been of little help in taxonomically placing the 'bald crow'. I have confirmed Lowe's description of *Picathartes oreas* with a fresh, but moulting, specimen of *P. gymnocephalus* (NYZS). It is of the typical oscine type, although with an exceptionally wide pars interscapularis; a broad, rounded and solidly feathered pars dorsalis; and a narrow pars pelvica. Ventrally, it has a wide pars pectoralis, well separated posteriorly from the pars abdominalis. In general strength, *Picathartes* surpasses the pterylosis of the few Timaliinae that have been studied (see above under Grallinidae) or of the small sample of Muscicapinae I have examined (briefly noted in Olson *et al.,* 1983). This is another instance of a bird, with the generalized oscine pattern, that cannot be placed by pterylosis except for being excluded from certain families (e.g., Corvidae, Sturnidae) that do have distinctive pterylosis patterns.

Sibley & Ahlquist, using a DNA-DNA hybridization technique, have begun to publish a series of papers that include many surprising suggestions on relationships within the Passeriformes (Sibley & Ahlquist, 1982; in

Fig. 12. *Corvus brachyrhynchos*, Pt. Ventralis. Typical passerine pattern of this tract, especially in type of separation between pars pectoralis and pars abdominalis.

press). It would be both premature and outside the scope of this paper to comment on many of their suggestions as to the relationships involving the Menurae and what has been called the corvid assemblage. Because I have seen only the bare classification, without the text, of the paper in press, I shall note only a few points.

Their Superfamily Menuroidea is made up of the Family Menuridae (*Menura, Atrichornis*), the Family Ptilonorhynchidae, and perhaps the Family Climacteridae. *Climacteris affinis* has a pars dorsalis that is long, lanceolate and heavily feathered (172 in ten rows in my single specimen, from a BM(NH) alcoholic). This is unlike *Certhia familiaris* which has a more lightly feathered, and shorter and rounder pars dorsalis (105 feathers in nine rows in one fresh specimen from Connecticut), and is very unlike *Rhabdornis inornatus* and *R. mysticalis* (three specimens of the genus, one from CM, two from USNM) which have a large apterium in the pars dorsalis. Sibley & Ahlquist may be correct in their suggestion about *Climacteris,* for the general type and shape of the pars dorsalis is not unlike that of *Menura,* considering the great difference in body size between them, but the Pt. Ventralis shows almost nothing distinctive (maximum width of 8 feathers, a rather long, separated pars pectoralis of seven rows, and abdominal rows with 5 feathers). The general pterylographic similarity of *Climacteris* to other oscines such as *Sitta* is at least as reasonable.

Sibley & Ahlquist (in press) erect a large Superfamily Corvoidea which is separated from the Menuroidea by the Superfamily Meliphagoidea; their Corvoidea includes a wide array of crows and their traditional allies, most of which have been discussed here. The birds-of-paradise are listed as a tribe immediately after the tribe of crows and jays, and immediately before the 'Cracticini, *Artamus, Strepera,* etc.', and then the orioles and cuckoo-shrikes. Sibley & Ahlquist also include in their Corvoidea a group of Old World, especially Australasian, groups that have hitherto been included in other (often 'wastebasket') families such as the Muscicapidae (s.l.) and Timaliidae. The few specimens I have representing these groups (e.g., *Pachycephala flavifrons*) have the common oscine pterylosis pattern that is no help in elucidating relationships.

Sibley & Ahlquist (in press) also include several groups as *incertae sedis* within their Corvoidea — the shrikes, the vireos and allies, and *Irena, Aegithina* and *Melanocharis.* The shrikes have already been discussed here. *Vireo* pterylosis is not unlike that of some of the traditional corvid allies and very unlike that of the New World, nine-primaried oscines. The latter have the typical and undistinguished oscine pattern, with minor exceptions. The vireos, in contrast, have a pars dorsalis that is nine or ten rows long, with the posteriormost three rows gapped away from the midline feathers which tend to be small or sometimes absent, forming a basal apterium. Whether or not a true apterium exists, the general vireo configuration is that of a lobed pars dorsalis, barely connected to an anteriorly weak pars pelvica. I have examined 10 specimens of *Vireo* (seven species, and including both subgenera *Vireo* and *Vireosylva*), and one specimen each of *Hylophilus flavipes, Vireolanius pulchellus* and *Cyclarhis gujanensis.*

Urik (1983) has studied *Irena* and *Aegithina,* as have I, and the pterylosis is not distinctive enough (a solidly feathered, lanceolate-to-rhombic pars dorsalis) to show relationships. I have also examined one specimen of *Melanocharis nigra* which has a pars dorsalis that is small (nine rows, 129 feathers), rounded and slightly lobed, without an apterium. The pars pelvica is weak anteriorly, producing the superficial appearance of a discontinuity between the pars dorsalis and pars pelvica.

Melanochar[illegible] comments about the Sibley & Ahlquist c[illegible]mall (nine r[illegible]the starlings are far removed from the c[illegible]obed, withou[illegible] indeed, are included in the Parvorder M[illegible]nteriorly, pr[illegible] whereas all the others already noted (inc[illegible]ontinuit[illegible]le Menuridae) are in the Parvorder Corvi; and Sibley recants somewhat from his previous opinion, based on egg-white protein and other evidence, that *Menura* (and he presumed *Atrichornis,* for which he then had no material) is most closely related to the 'bowerbird/bird-of-paradise assemblage' (Sibley, 1974). He stated in the earlier paper (1974: 78) that "*Menura* is more closely related to the bowerbirds than to the birds-of-paradise, although all three groups are members of a single natural cluster". In the new DNA study, the bowerbirds (with the Menuridae) are far removed from the birds-of-paradise.

DISCUSSION AND CONCLUSIONS

In this study of 154 specimens representing 126 species of 98 genera, I have attempted to compare the body pterylosis of *Atrichornis* and *Menura* with that of all the passerine groups to which they might conceivably be related. The availability and quality of specimens put some constraints on these comparisons because I could not locate satisfactory (or any) material of some of the genera I would like to have looked at, but I believe there are no serious lacunae in the present series. The most important pterylographic findings are summarized in Table 4.

Within this series, *Atrichornis* and *Menura* are singular in many respects. They have extremely dense feathering, both dorsally and ventrally. Their pars dorsales of 228 feathers in *Atrichornis* and 656 in *Menura* are comparable in view of the great disparity in their body sizes — the *Atrichornis* weighed 34 g and the *Menura* 921 g (both were females). They show the same basic passerine patterning in the Pt. Spinalis, similarly modified to accommodate their extraordinary number of feathers. The small gap they both have between the pars dorsalis and pars pelvica seems to be of some systematic importance. *Atrichornis* and *Menura* are less similar ventrally, with the scrub-bird having a very wide pars pectoralis (17 feathers at the maximum)

Taxon (with No. Genera Studied)	Pt. Spinalis, Pars Dorsalis: Length (rows)	Tot. No. Feathers	Apterium	Pt. Ventralis: Max. Width	Free Pect. Rows	Width Abdom. Rows
Atrichornis	12	228	D/P gap[1]	17	2	5
Menura	18	656	D/P gap	c.13	10	4
Paradisaeidae						
Cnemophilinae (3/3)	c.13	225–254	no	9	3–4	4
Paradisaeinae (14/17)	7–10	83–180	gap, D/P gap, or weakness	7–28[2]	3–7	3–5
Astrapia	11	200–201	gap or 1-row apt.	13–14	5–6	5
Ptilonorhynchidae (6/8)	11–15	180–281	5–10 rows	10–11	2–4	4–6
Turnagra	c.15	300–327	none apparent	11	4	4–5
Grallinidae (3/3)						
Grallina	9	–	3 rows	[illegible]	8	5
Struthidea, Corcorax	9	119	slight g[illegible]D/P	7–2[illegible]	5	4–5
Artamidae (1/1)	c.11	–	no [illegible], or		4	5
Callaeidae (2/3)	14	298	gap [illegible]kness		0	4
Cracticidae (2/3)	10–11	198–201	gap, 1-ro[illegible]-row apt., or D/P gap	13[illegible]1	5	5
Oriolidae (1/2)	12	234	no	9	5	6
Dicruridae (1/2)	c.9	–	2 rows	8	3	–
Laniidae (4/21)	8–10	126–129	slight gap	9–10	3–6	4–5
Sturnidae (19/26)	5–9	47–136	gap or 1–3 rows; characteristic pattern	8–11	3–5	4–6
Corvidae (26/26)	9–13	110–198	2–8 rows, a few with gaps, or no apt.	8–21	3–8	3–5
Ptilostomus	8	90	no	9	4	4
Platylophus	6	50	no	7	4	3

Table 4. Summary of pterylographic differences.

[1]D/P gap = gap between pars dorsalis and pars pelvica; other gap notations refer to the posterior rows and midline area of the pars dorsalis.

[2]7–10 rows in spp. without ventral plumes, 11–28 in spp. with ventral plumes.

and a short (two-rowed) separation of the pars abdominalis from the pars pectoralis; the separation is otherwise typically passerine. *Menura* differs strikingly in this separation, having a pattern that is unique within the Passeriformes, insofar as is known. The lyrebird is also generally heavily feathered below, with a maximum width of the pars pectoralis of approximately thirteen rows.

As I have stated earlier (Clench, 1970), the taxonomic significance of the number of feathers on a bird's body (but not the pattern of feather insertion) must be assessed in light of the overall body size. This is easy to do in a subjective manner but difficult to accomplish with precision because of the problems involved in measuring body size accurately. The three customary body size measurements (overall length, wing length, or weight) all present problems when considering a group of birds with the wide diversity present here. Weight is probably the most accurate measure, even given its natural variation — the differences in a single individual's weight throughout a day, week, season or year (Clench, unpublished data). The fact remains, however, that not until recent years has a specimen's weight become a standard label datum, and even single weight records do not exist in the published literature for the majority of the species treated here. Wing length is a more available datum, but it would be highly misleading to compare the wing length/pterylographic counts of such birds as *Atrichornis* and *Menura,* which are notoriously weak fliers and short-winged, with most of the birds in the 'corvid assemblage', which have normal powers of flight and proportionately longer wings. One is left, then, with overall body measurement to try to compare with pterylosis density. Again, difficulties arise because *Menura* and some of the birds-of-paradise have extraordinarily long plumes or tails. I have tried, however, to use conservative measurements to achieve a rough numerical index of feather density (the number of feathers in the pars dorsalis/overall body length in mm).

The species or generic groups that have the heaviest feathering are *Climacteris* (1.23), *Turnagra* (1.18), the Cnemophilinae (1.12), *Atrichornis* (0.99), *Oriolus* (0.88), *Certhia* (0.81), *Menura* and the

Ptilonorhynchidae (both 0.77), and the Callaeidae (0.70). The index figure for *Menura* is probably artificially low, weighted by the extremely long tail, even of females. Those with an intermediate degree of feathering are *Lanius* (0.53), the Cracticidae (0.51) and *Astrapia* (0.48). Birds with light feathering are *Struthidea* (0.36), the Corvidae (0.35), the Sturnidae (0.30) and the Paradisaeinae (0.20). I urge that not too much importance be placed on these figures, based as they are on broad averages of body length and limited numbers of feather counts, but I believe they offer at least a rough index to the degree of body feathering.

To further assess the general accuracy of this method, I computed the indices for several New World corvids for which data were readily available. Members of the first group (crows, Old World jays and allies, that were grouped on the basis of pterylographic pattern) gave similar index numbers: *Pica* (0.34), *Corvus ossifragus* (0.28), *Corvus brachyrhynchos* (0.36) and *Corvus corax* (0.32). The three species of *Corvus* were originally selected for the series because they represented the wide range of variation in body size seen in this genus, yet their index values were within 0.08 of each other. A similar calculation of the *Corvus* series, based on body weight, also resulted in close values — within 0.10. The single exception in the series of New World members of the first group was *Nucifraga;* nutcrackers had heavier feathering (0.52). All of the genera of the second group tested (New World jays) gave similar values: *Cyanocitta* (0.56), *Aphelocoma* (0.58), *Gymnorhinus* (0.51) and *Cyanocorax* (0.55).

Many genera in the full comparative series showed dense feathering like that of *Atrichornis* and *Menura* — the cnemophiline birds-of-paradise, the bowerbirds, *Turnagra, Climacteris* and the Callaeidae (Table 4). These groups, and the related Paradisaeinae, also show pattern similarities in aspects of their pterylosis that may suggest a relationship, although not a very close one. The Cnemophilinae are generally similar in dorsal feathering, both in density and pattern. Certain of the Paradisaeinae have a pars pectoralis/pars abdominalis separation that is suggestive of, but not precisely the same as, that in *Menura,* and the entire subfamily has a weakness in the base of the pars dorsalis, including a small gap in some genera. The Callaeidae also have a heavily feathered pars dorsalis with a basal gap, but they lack any separation at all between the pars pectoralis and pars abdominalis (unique within oscines, in my experience, but found in a few suboscines, notably in all the Rhinocryptidae I have studied except *Melanopareia). Turnagra* most closely resembles the cnemophiline birds-of-paradise, as I have stated earlier (Olson *et al.,* 1983).

The primary conclusion from this study is that *Menura* and *Atrichornis* are each other's closest relatives, but the degree of similarity is such that they should remain separated taxonomically, at least in different families. In turn, their closest relationships lie with the Paradisaeidae-Ptilonorhynchidae-Callaeidae complex. Again, the degree of similarity is not close, but is closer than it is to any other group of passerines.

Other pterylographic findings of this study are: 1) if the 'corvid assemblage' is a strong natural entity, it is not apparent from pterylography. The true Corvidae generally have a well developed basal apterium in the pars dorsalis that I have not found elsewhere in oscines except in the Ptilonorhynchidae and *Grallina,* although a less well developed apterium, gapping, or basal weakness occurs in the Paradisaeinae, *Struthidea* and *Corcorax,* the Cracticidae, Sturnidae, Vireonidae, Laniidae and Dicruridae. A small apterium or gapping is also found in a few other, clearly unrelated oscines (e.g., Dicaeidae, *Arachnothera* but not *Nectarinia, Pl[illegible]* but not other weavers, and some Sylviinae) as [illegible] shows this [illegible]rtain suboscines. Other types of apteria [illegible]o core genei[illegible] the Alaudidae, Hirundinidae and many [illegible]sts that *Astro* suboscines (Heimerdinger, 1964). 2) [illegible] entire bird *A[illegible]hus* is r[illegible]as a somewhat unusual pterylosis; it lies between the normal pattern for paradisaeines and cnemophiline birds-of-paradise, but also may show a small apterium, possibly reminiscent of bowerbirds. In his diagram of paradisaeine relationships, Schodde (1976) shows this genus (along with *Lophorina*) as one of two core genera for the subfamily. Pterylography suggests that *Astrapia* may be a bit deeper into the core of the entire bird-of-paradise/bowerbird complex. 3) *Platylophus* is not a corvid and *Ptilostomus* is probably not, either. *Ptilostomus* may be an aberrant starling. 4) *Grallina* shows no pterylographic relationship to *Struthidea* and *Corcorax;* the old family 'Grallinidae', constituting these three genera, should be abolished. Although the pterylosis does not strongly suggest affinities that would assist in new placements, *Grallina* shows no similarities to motacillids, but *Struthidea* and *Corcorax* may be babblers.

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Pterylosis of the Wing and Tail in the Noisy Scrub-Bird, *Atrichornis clamosus*, and Superb Lyrebird, *Menura novaehollandiae* (Passeriformes: Atrichornithidae and Menuridae)

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ABSTRACT. The wing and tail pterylosis of *Atrichornis clamosus* and *Menura novaehollandiae* were studied. On comparing the wing pterylosis, a great difference was found in the number of the remiges and coverts, especially those in the forearm. In comparison with *Ploceus nigerrimus* (Morlion, 1971), chosen as a representative passerine, we saw that in wing pterylosis *Atrichornis* is much nearer to the Passeres than is *Menura*.

In the tail pterylosis, a great difference also exists between the two species investigated: not only in the aspect of the feathers, but also in the number of rectrices, greater upper and under tail coverts and in the presence or absence of the first pair of upper and under tail coverts. In contrast to the wing pterylosis, however, the tail pterylosis of *Atrichornis* is markedly different from *Ploceus nigerrimus*.

MORLION, M.L., 1985. Pterylosis of the wing and tail in the Noisy Scrub-bird, *Atrichornis clamosus*, and Superb Lyrebird, *Menura novaehollandiae* (Passeriformes: Atrichornithidae and Menuridae). Records of the Australian Museum 37(3): 143–156.

KEYWORDS: comparative morphology, pterylosis, Atrichornthidae, Menuridae, Aves.

The wing and tail pterylosis of *Atrichornis clamosus* and *Menura novaehollandiae* were investigated using the clipping method (Morlion, 1971). Because the tips of the remiges and rectrices of the *Menura* specimen were worn, only the measurements of the wing and tail feathers of *Atrichornis* could be taken.

A. Alar tract

Figs 1–9, Table 1

1. Primaries. In *Atrichornis*, ten well developed primaries are present. All of the remiges overlap laterally in the same way: the distal (outer) vane of each remex overlaps the proximal vane of the next distal feather. The diameter of the calamus gradually decreases outwards; the last two primaries have a markedly smaller rachis. Neighbouring downy feathers are absent on both sides of the wing. On the dorsal side, the first four primaries are accompanied by two proximal filoplumes (6 mm long), the fifth and sixth primaries have only one proximal filoplume, and the rest have none. On the ventral side, no filoplumes are found near the primaries.

Menura possesses eleven primaries: ten are well developed and the eleventh is weaker. In this feature, *Menura* differs from most Passeres and resembles many non-passerines. Other passerines known to have eleven primaries include *Corvus* (Morlion & Vanparijs, 1979). From the innerside to the tip of the hand, the calamus diameter of the primaries gradually decreases. All of the remiges overlap laterally as in *Atrichornis*. On the dorsal side of the wing near the base of each of the primaries, three downy feathers are found, one or two of them lying in the skin fold between the primaries. Filoplumes are absent. On the ventral side of the wing, Prim. I up to Prim. III, inclusive, have on their proximal side a downy feather inserted on the skin fold and under the corresponding upper greater primary covert. Prim. IV up to Prim. IX, inclusive, have a proximal downy feather over their calamus. Prim. X has no proximal, but four distal downy feathers.

2. Secondaries. In *Atrichornis* there are nine secondaries, as in most Passeres. They show the same overlapping as the primaries and lie parallel with each

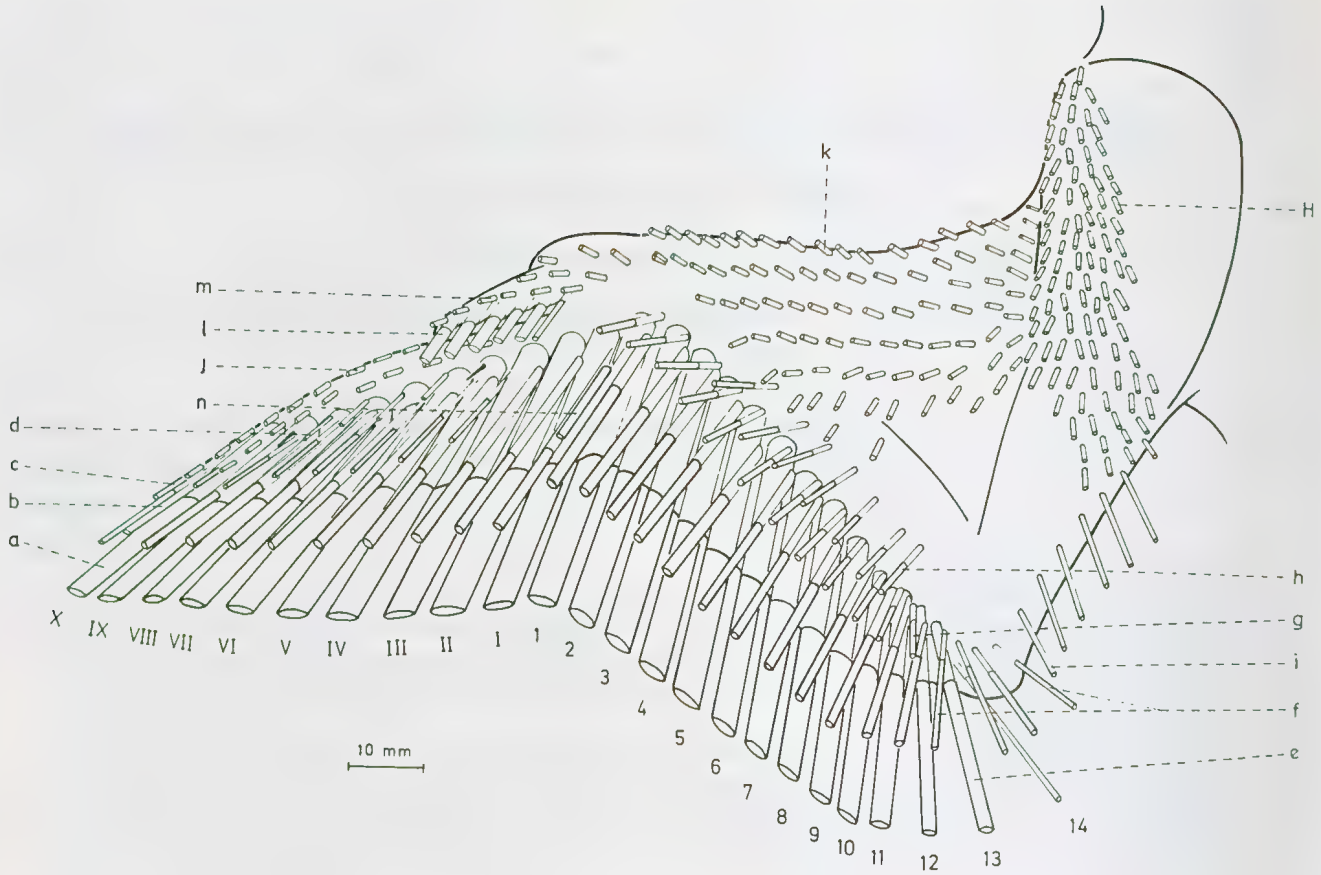

Fig. 1. Pterylosis of the wing of *Menura novaehollandiae*: dorsal view.
a. primaries (numbered I–X)
b. upper greater primary coverts
c. upper middle primary coverts
d. upper lesser primary coverts
e. secondaries (numbered 1–14)
f. upper greater secondary coverts
g. upper middle secondary coverts
H. pteryla humeralis
h. upper lesser secondary coverts
i. tertiary coverts
j. upper carpometacarpal coverts
k. upper marginal coverts
l. alula quills
m. alula coverts
n. carpal covert

other. The calamus diameter decreases from the distal part of the forearm, inward. On the dorsal side of the wing, neither downy feathers nor filoplumes accompany the secondaries. On the ventral side of the wing, only the first two secondaries have a proximal filoplume, both of which originate from a distinct papilla. Near the other secondaries, downy feathers and filoplumes are completely missing.

In *Menura*, the secondaries are fourteen in number, much more numerous than in most Passeres, which usually have nine. Sibley (1974) reported only ten secondaries in *Menura*. From Sec. 11 to Sec. 14, a marked decrease in calamus diameter occurs. The fourteenth secondary is rather thin and it does not insert on the border of the underarm, but lies slightly dorsal to the others. The wing is eutaxic. The proximal secondaries spread open, fan-like. On the dorsal side of the wing, three downy feathers insert between each of the first six secondaries and their corresponding upper greater secondary coverts; between the seventh to the tenth secondaries and their coverts, two downy feathers are found; between the eleventh secondary and its covert only one is found; and the remaining secondaries have no downy feathers at all. A few irregularly spaced filoplumes can be found mediodorsal to the secondaries. On the ventral side of the wing, some secondaries have one or two very short, 3 mm long, filoplumes. The downy feathers found proximal to Sec. 9 through Sec. 13 could represent vestigial under greater secondary coverts.

3. Upper greater primary coverts. *Atrichornis* has ten upper greater primary coverts. They insert distally to and near the insertion of their corresponding primary. They form a very small acute angle with their remiges; only the last ones are nearly parallel with the primaries. The coverts overlap in the same way as the primaries. The barbs of the vane converge medially and there is a very weak hyporachis consisting of just a few filaments. No downy feathers or filoplumes are found, except for the ninth and tenth upper greater primary

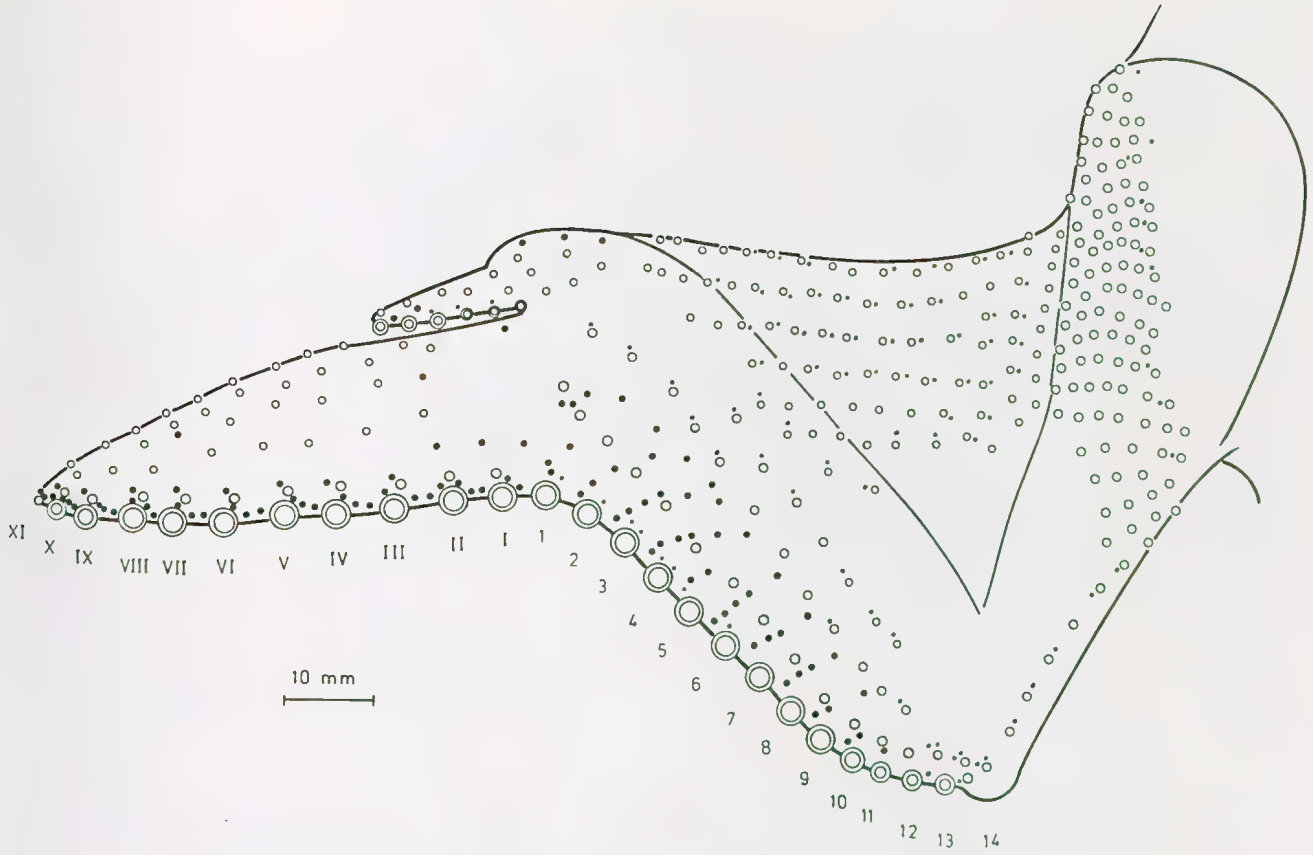

Fig. 2. Pterylosis of the wing of *Menura novaehollandiae*: dorsal view.
ⓞ remex
o covert
● downy feather
• filoplume

coverts which possess one distal filoplume each.

Menura has ten well developed upper greater primary coverts. They insert over the distal half of the calamus of the corresponding primary. Prim. XI has no upper greater primary covert. The calami of these coverts lie parallel to each other and caudodistally to the calamus of the corresponding primary, making a small acute angle with the latter. They have the same overlap as the primaries. With the exception of the first two, each greater primary covert possesses a distal downy feather. These coverts do not have a hyporachis but the two sides of the vane converge medially on the calamus.

4. Upper greater secondary coverts. In *Atrichornis* the number of upper greater secondary coverts outnumbers the number of secondaries by one. Each of these ten coverts inserts distally to its corresponding secondary and forms a distinct acute angle with it. This angle is very small for the eighth upper greater secondary covert, while the ninth covert runs nearly parallel to its secondary. Here too, the barbs converge medially and a very weak hyporachis is found. No downy feathers are present but each covert possesses a distal filoplume (up to 12 mm long).

There are sixteen upper greater secondary coverts in *Menura*. All of the secondaries possess a greater secondary covert inserted halfway up their calamus and on the distal half. Only the fourteenth inserts just dorsally of its corresponding secondary. The two 'additional' upper greater secondary coverts (without a corresponding secondary) have a stronger rachis and different orientation, easily distinguishable from the tertiary coverts. All these coverts show a caudodistal orientation. Only the last three exhibit a more caudoproximal direction. These coverts lack a hyporachis. Most of them are accompanied by a distal downy feather and the last three possess two distal filoplumes each.

5. Upper middle primary coverts. In *Atrichornis*, seven pennaceous and one downy upper middle primary coverts are found. Coverts associated with the ninth and tenth primaries are missing and the eighth is downy. The upper middle coverts insert distally to the upper greater primary coverts and lie parallel to them. These little feathers are too small to overlap each other. Some of them lack pigment. They have a very weak hyporachis. Neither downy feathers nor filoplumes are found in their surroundings.

Eight upper middle primary coverts are present in *Menura*. Near Prim. I up to Prim. III, inclusive, they are lacking, but a downy feather inserts at the lower third of the calamus. The eight following upper greater primary coverts each have an upper middle covert. The

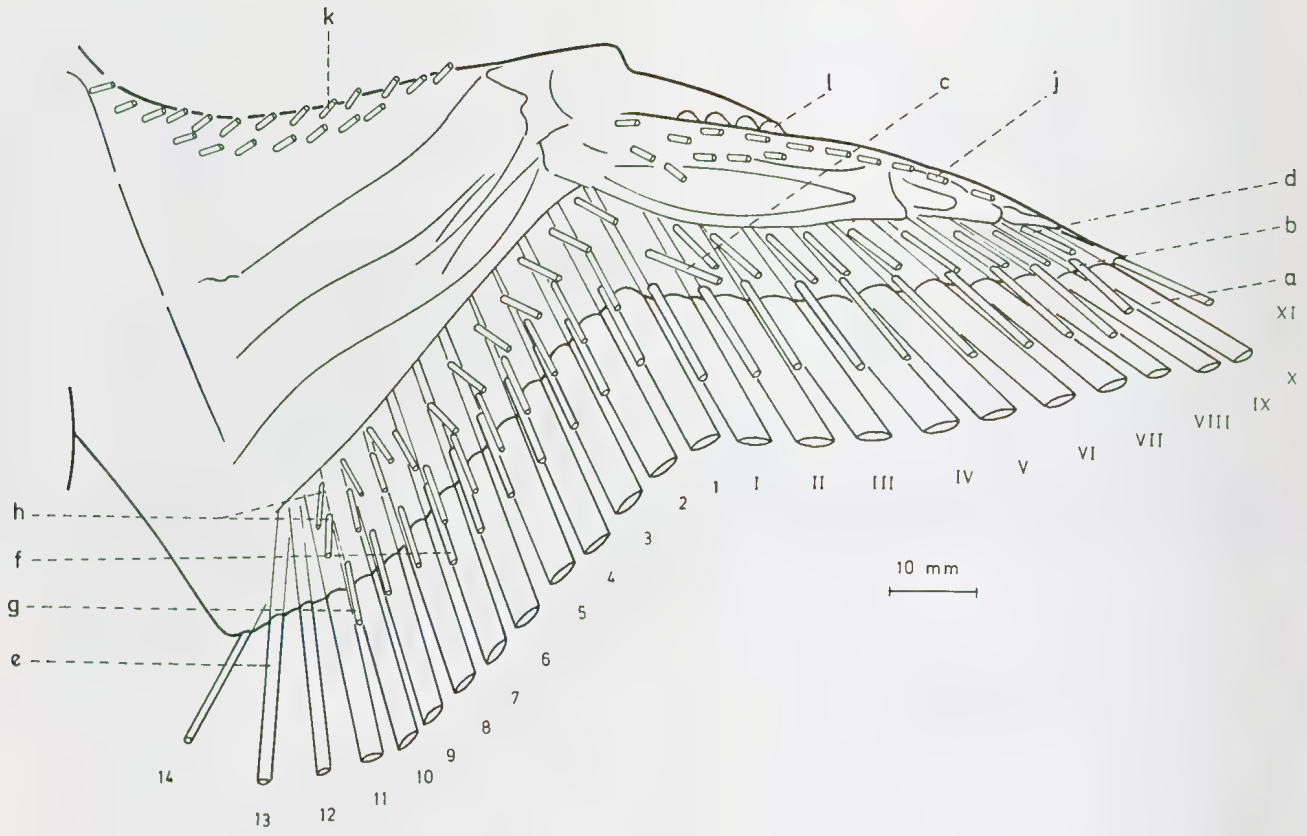

Fig. 3. Pterylosis of the wing of *Menura novaehollandiae*: ventral view.
a. primaries (I–XI)
b. under greater primary coverts
c. under middle primary coverts
d. under lesser primary coverts
e. secondaries (1–14)
f. under greater secondary coverts
g. under middle secondary coverts
h. under lesser secondary coverts
j. under carpometacarpal coverts
k. under marginal coverts
l. alula quills

insertion of these latter coverts is somewhat different from that usually found in the Passeres. In *Menura* they insert over the proximal half of the corresponding primary calamus and lie proximally and parallel to the corresponding upper greater primary covert. They have a slightly caudo-proximal orientation, forming a small acute angle with the primaries. They lack both a hyporachis and accompanying downy feathers or filoplumes.

6. Upper middle secondary coverts. In *Atrichornis* the first of the eight upper middle secondary coverts is downy, the other seven are little quills. They insert near the end of the calamus of the corresponding secondary, and distally to this secondary and its upper greater secondary covert. The first upper middle secondary coverts form a small acute angle with the upper greater secondary coverts, the last ones lie parallel to them. The last two have a notably smaller rachis. A very weak filamentous hyporachis is found in the middle of the converging barbs. No downy feathers or filoplumes are found in their surroundings.

There are twelve upper middle secondary coverts in *Menura*. Sec. 13 and Sec. 14 have none. These coverts insert on the distal side of the calamus of the corresponding secondary and the upper greater secondary covert. Initially they are caudodistally oriented but the last one is caudally directed. They lack a hyporachis. Most of them are accompanied by a distal filoplume. Between the insertions of each set of corresponding greater and middle secondary coverts, one or two downy feathers are found.

7. Upper lesser primary coverts. The upper lesser primary coverts are completely missing in *Atrichornis*. In *Menura*, one proximally incomplete row of four well developed and two downy (the most proximal and the most distal) upper lesser primary coverts is present. Distally these coverts are continuous, by way of that distal downy feather with the upper carpometacarpal coverts. The upper lesser primary coverts lack a hyporachis. As far as it is known, these feathers are completely missing in all other Passeres.

8. Upper lesser seondary coverts. In *Atrichornis*, the upper lesser secondary coverts consist of an incomplete row of seven downy feathers. One incomplete row of seven well developed upper lesser secondary coverts is found in *Menura*. They lack a hyporachis. A distal

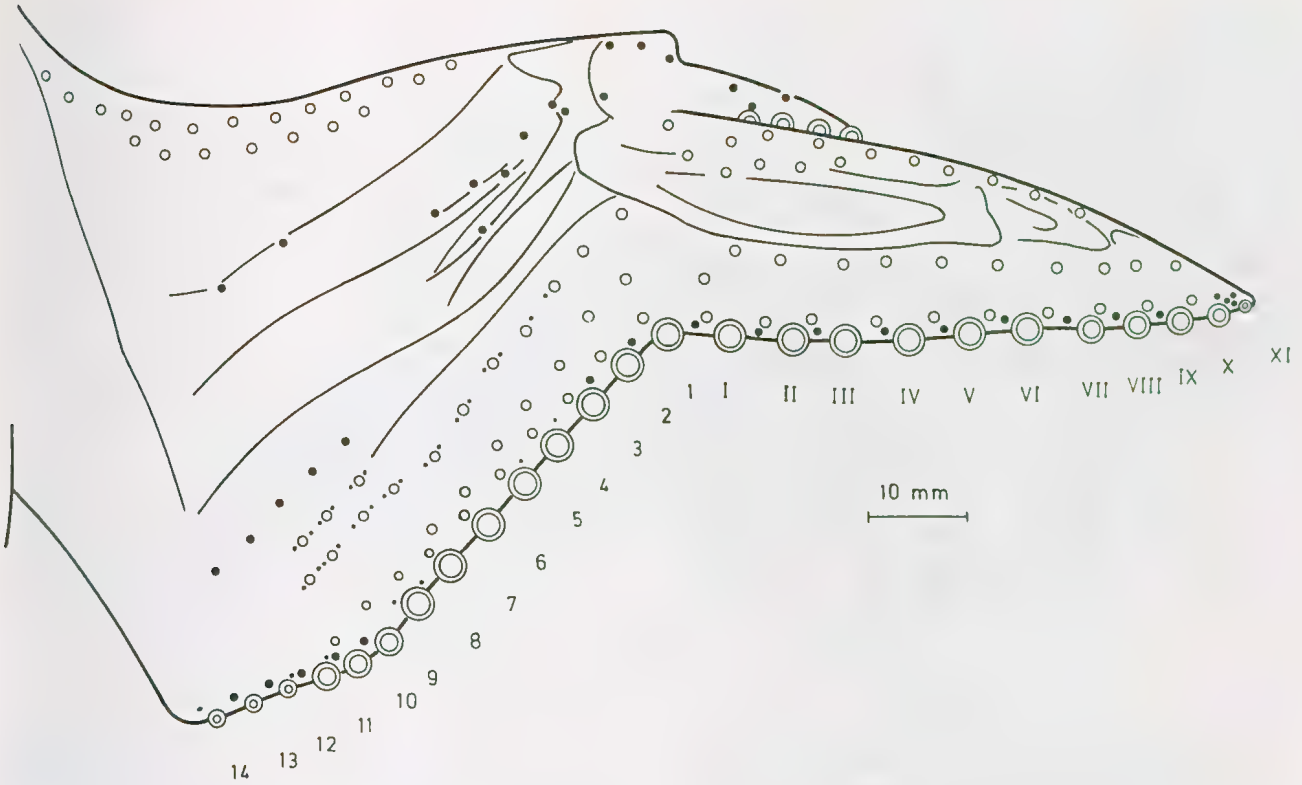

Fig. 4. Pterylosis of the wing of *Menura novaehollandiae*: ventral view.
◎remex
o covert
● downy feather
• filoplume

filoplume is found near all but one of them.

9. Tertiary coverts. In *Atrichornis* there is a double row of tertiary coverts, inserted and oriented parallel to the caudal border of the upper arm. The upper row consists of four feathers with a distinct downy hyporachis and an accompanying distal filoplume. The four feathers of the lower row have the same kind of hyporachis but lack filoplumes.

There is a single row of six tertiary coverts in *Menura*. They are accompanied by a distal or a proximal filoplume. A hyporachis is lacking. Proximally they are continuous with the humeral coverts; distally they touch the upper greater secondary coverts.

10. Upper carpometacarpal coverts. A double row of upper carpometacarpal coverts inserts at the foremost border of the hand in both species. The most peripheral row inserts on the hand border. The feathers are oriented parallel to that border. In *Atrichornis*, these coverts are preceded by one or two downy feathers and all the coverts have a weak filamentous hyporachis. They lack a hyporachis in *Menura novaehollandiae*. No downy feathers or filoplumes are found in their surroundings.

11. Upper marginal coverts. The upper marginal coverts are not very numerous in *Atrichornis*. They form a lozenge pattern on the propatagium. The little pennaceous feathers of the most cranial row alternate with downy feathers. Otherwise no other downy feathers are found among them. Most coverts are anterodistally oriented; only the more caudally inserted quills are posterodistally directed. The marginal coverts have a weak hyporachis and have a distal filoplume.

The upper marginal coverts are very numerous in *Menura*. Their insertions form a lozenge pattern on the propatagium. Horizontal and oblique rows can be distinguished. Most coverts have a filoplume in their immediate vicinity. Proximally, the marginal coverts are continuous with the humeral coverts but can be distinguished by a different orientation. Distally a small apterium separates them from the alula coverts. Most marginal coverts are anterodistally oriented; only the feathers of the lowest row are posterodistally directed. A hyporachis is absent.

12. Under greater primary coverts. In *Atrichornis* there are ten pennaceous and one downy under greater primary coverts. They insert very near the insertions of the primaries and just proximal to them. Distally to the first two is a filoplume originating from a distinct papilla. Downy feathers are completely absent in their vicinity. The first under greater primary covert has a stronger rachis than the others. All of them possess a distinct but weak hyporachis.

In *Menura* too, ten under greater primary coverts insert near the base, and lie on the proximal side, of the calamus of the corresponding primary. The proximal coverts lie parallel to the primaries; more distally, they

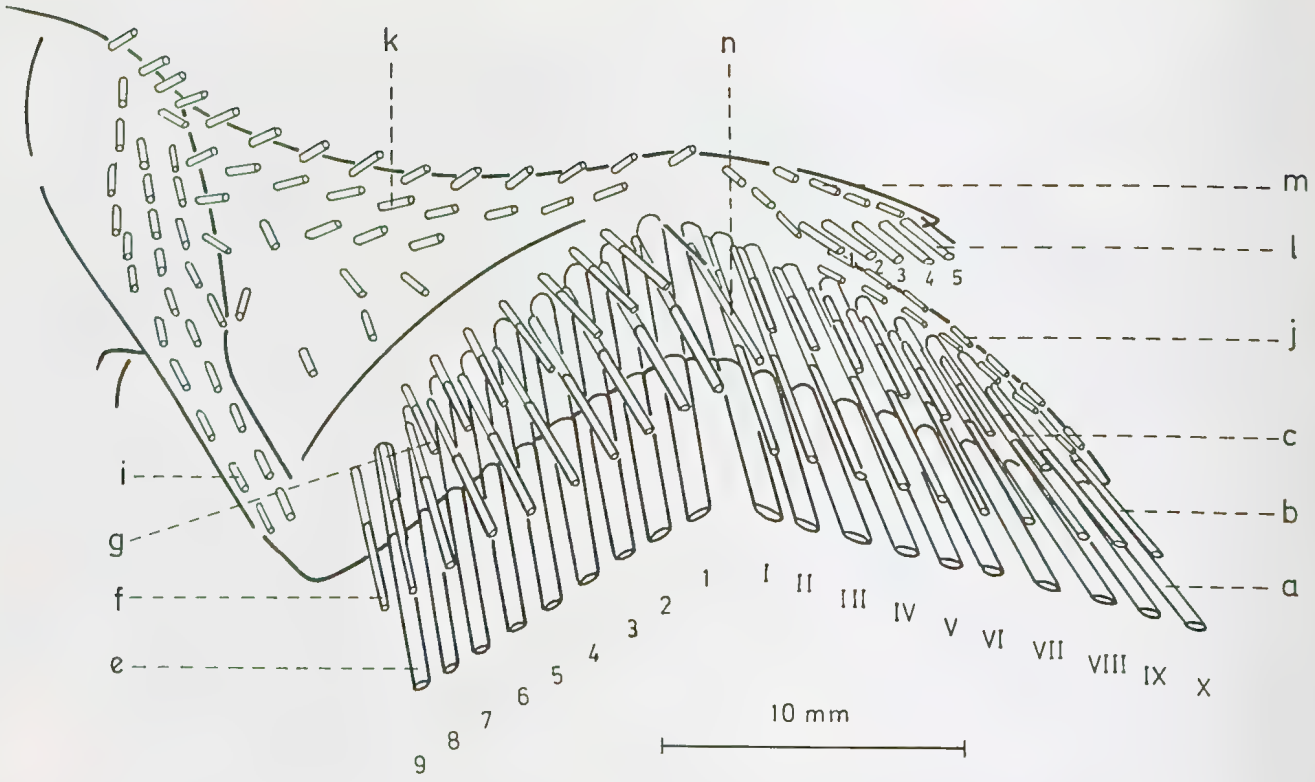

Fig. 5. Pterylosis of the wing of *Atrichornis clamosus*: dorsal view.
a. primaries (I–X)
b. upper greater primary coverts
c. upper middle primary coverts
e. secondaries (1–9)
f. upper greater secondary coverts
g. upper middle secondary coverts
H. pteryla humeralis
i. tertiary coverts
j. upper carpometacarpal coverts
k. upper marginal coverts
l. alula quills (1–5)
m. alula coverts
n. carpal covert

exhibit a slightly oblique course, forming a small acute angle with them. All these coverts are well developed and do not have a hyporachis. Externally, their calamus is not visible. A weak, downy feather inserts at the place of the eleventh under greater primary covert. These coverts are not accompanied by either downy feathers or filoplumes.

13. Under greater secondary coverts. The under greater secondary coverts are completely absent in *Atrichornis*. In *Menura*, there are seven pennaceous under greater secondary coverts, inserted proximally to their corresponding secondaries and oriented parallel to them. The first four coverts are plain quills and the following three are less developed and somewhat downy quills. Near the eighth secondary, no proximal covert is found but, proximal to the ninth and up to the thirteenth, a downy or even very weak downy feather is present. Perhaps these can be considered as vestigial under greater secondary coverts. No filoplumes or other downy feathers are found in the surroundings of these feathers. In the Passeres the under greater secondary coverts are usually absent and, if present, they are small and rudimentary downy feathers.

14. Under middle primary coverts. In *Atrichornis*, the first under middle primary covert is the only one present. It inserts proximally to the first primary and the first under greater secondary covert, and lies parallel to them. It has a distinct filamentous hyporachis.

The first under middle primary covert is also the only one present in *Menura*. It has an obvious oblique orientation, is posterodistally directed, and forms an acute angle with the first primary. Its insertion lies halfway down the calamus of this primary. There are no accompanying filoplumes or downy feathers.

15. Under middle secondary coverts. There are eight pennaceous under middle secondary coverts and a ninth downy one in *Atrichornis*. The first two lie on the proximal side of the calamus of the corresponding secondary; the others undergo a slight proximal shift so that they are not situated on, but lie next to the calamus at its proximal side. Their course is parallel to that of the corresponding secondary. Proximal to each quill, a papilla is found and, near the sixth, seventh and eighth under middle secondary covert, a filoplume is inserted in the papilla. No downy feathers are present in the vicinity. Some weak filaments constitute a

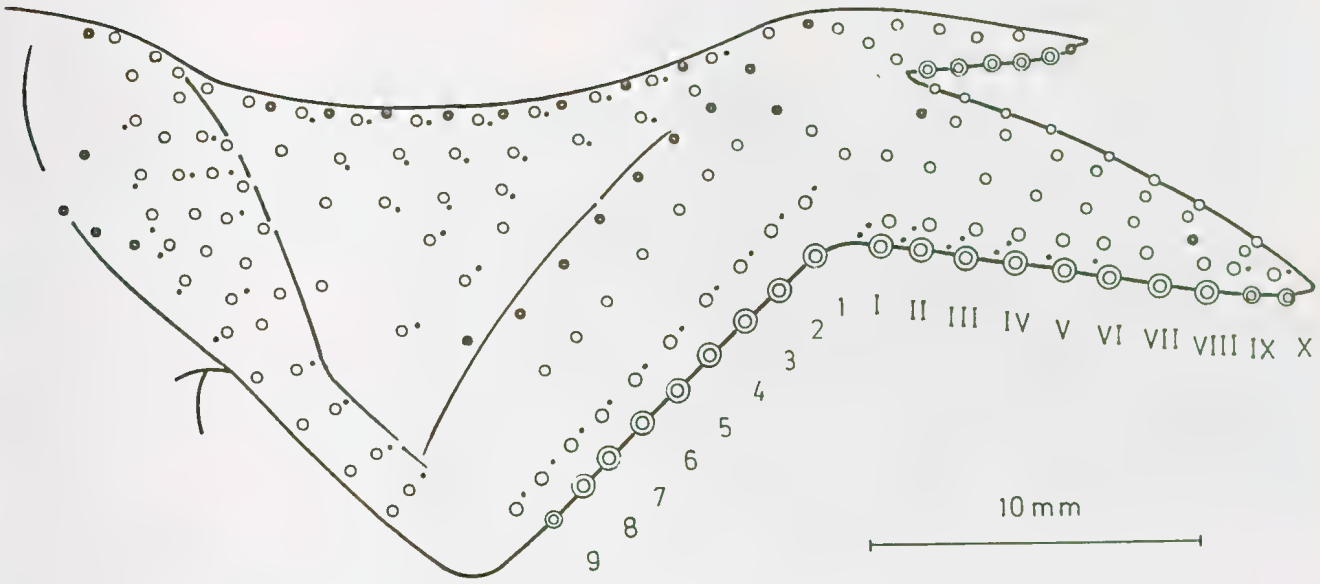

Fig. 6. Pterylosis of the wing of *Atrichornis clamosus*: dorsal view.
◎ remex
o covert
• downy feather
• filoplume

hyporachis.

In *Menura* the ten under middle secondary coverts insert proximally to their corresponding secondaries and lie parallel to them. Only the most proximal coverts show a slight change in orientation. No downy feathers or filoplumes are found near them. All the under greater and middle coverts are reversed: their concave, morphologically ventral side lies at the outside, and not inwards, as for the other coverts.

16. Under lesser primary coverts. In *Atrichornis* ten pennaceous, followed by one downy, under lesser primary coverts are found. They insert proximally to the corresponding primary and under greater primary covert, and form a small acute angle with them. They are weak, somewhat downy little quills; some of them lack pigmentation. They have a very weak, downy hyporachis. No downy feathers or filoplumes are found near them.

There are ten under lesser primary coverts in *Menura*. Each primary, except the first, has on the proximal side of its calamus an under lesser primary covert. The covert near the eleventh primary is less developed and somewhat downy. The coverts' rami converge medially, but a true hyporachis is lacking. Downy feathers and filoplumes are not present.

17. Under lesser secondary coverts. In *Atrichornis* there are three pennaceous and four downy under lesser secondary coverts. These little coverts are much weaker than those of the other series in the same bird. They insert proximally to their corresponding secondary and under middle secondary covert, and are slightly posterodistally oriented. Some of them lack pigmentation.

There are two rows of under lesser secondary coverts in *Menura*. The first row has eleven feathers; only near the last three secondaries are they missing. Most of the coverts have a filoplume on both sides. The second incomplete row has only three coverts, lying above the proximal end of the other row. A third, distally incomplete row of downy feathers is also present.

18. Under carpometacarpal coverts. In *Atrichornis*, the under carpometacarpal coverts consist of a single row of six little quills. They insert parallel to the border of the hand but are not oriented parallel to it. They have a weak, downy hyporachis. Downy feathers or filoplumes are not present in this area.

In *Menura* the under carpometacarpal coverts consist proximally of a double, but distally of a single, row of feathers, inserted and oriented parallel to the border of the hand. These coverts lack a hyporachis. Neither downy feathers nor filoplumes are found nearby.

19. Under marginal coverts. In *Atrichornis*, only one row of nine under marginal coverts is present. They insert very near to the anterior border of the propatagium, and the row of their insertion lies parallel to it, but the feathers are anterodistally directed. Each covert has a posterodistal filoplume and the most proximal one even has a supplementary little quill posterodistal to it. These coverts have a very weak hyporachis. A few downy feathers are sparsely distributed over the undersurface of the propatagium.

A double row of feathers situated at the anterior border of the propatagium forms the under marginal coverts in *Menura*. They insert parallel to the propatagium border, but are not oriented parallel to it. Some of them have a distal filoplume.

20. Under tertiary coverts. In *Atrichornis* three downy under tertiary feathers are present. *Menura* has

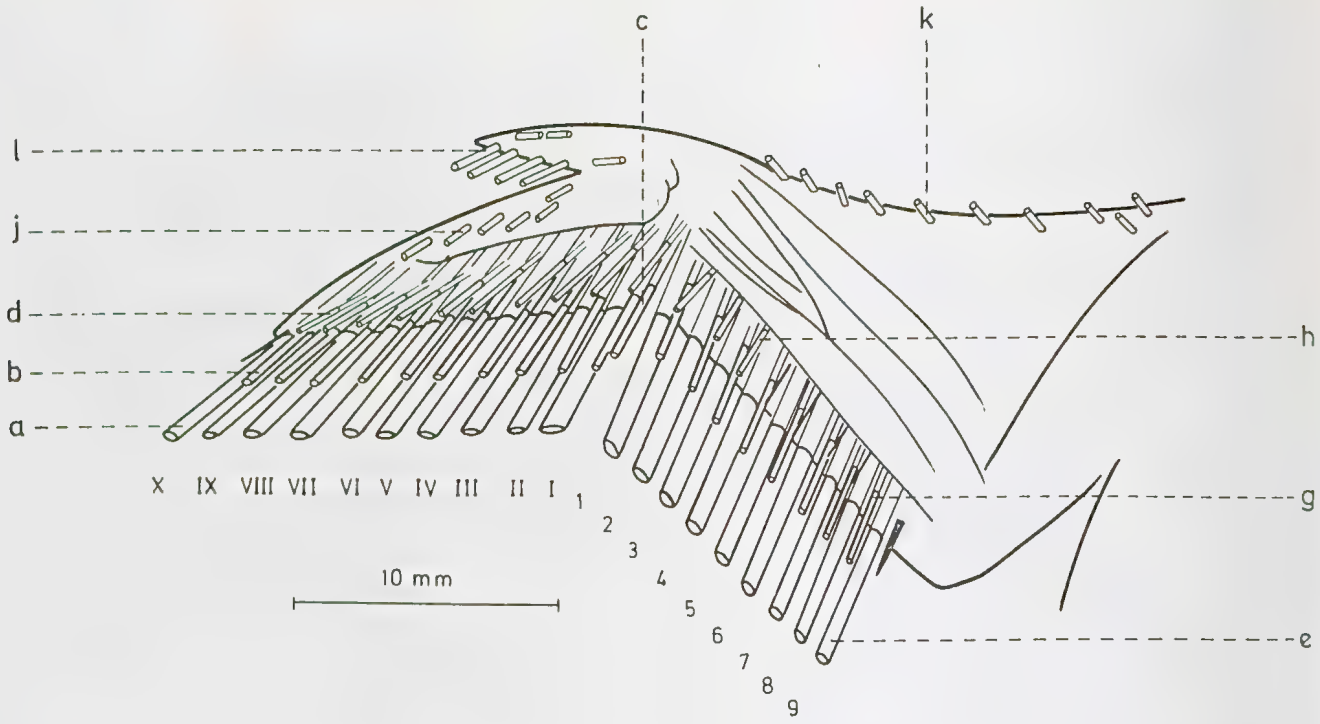

Fig. 7. Pterylosis of the wing of *Atrichornis clamosus*: ventral view.
a. primaries (I–X)
b. under greater primary coverts
c. under middle primary covert
d. under lesser primary coverts
e. secondaries (1–9)
g. under middle secondary coverts
h. under lesser secondary coverts
j. under carpometacarpal coverts
k. under marginal coverts
l. alula quills

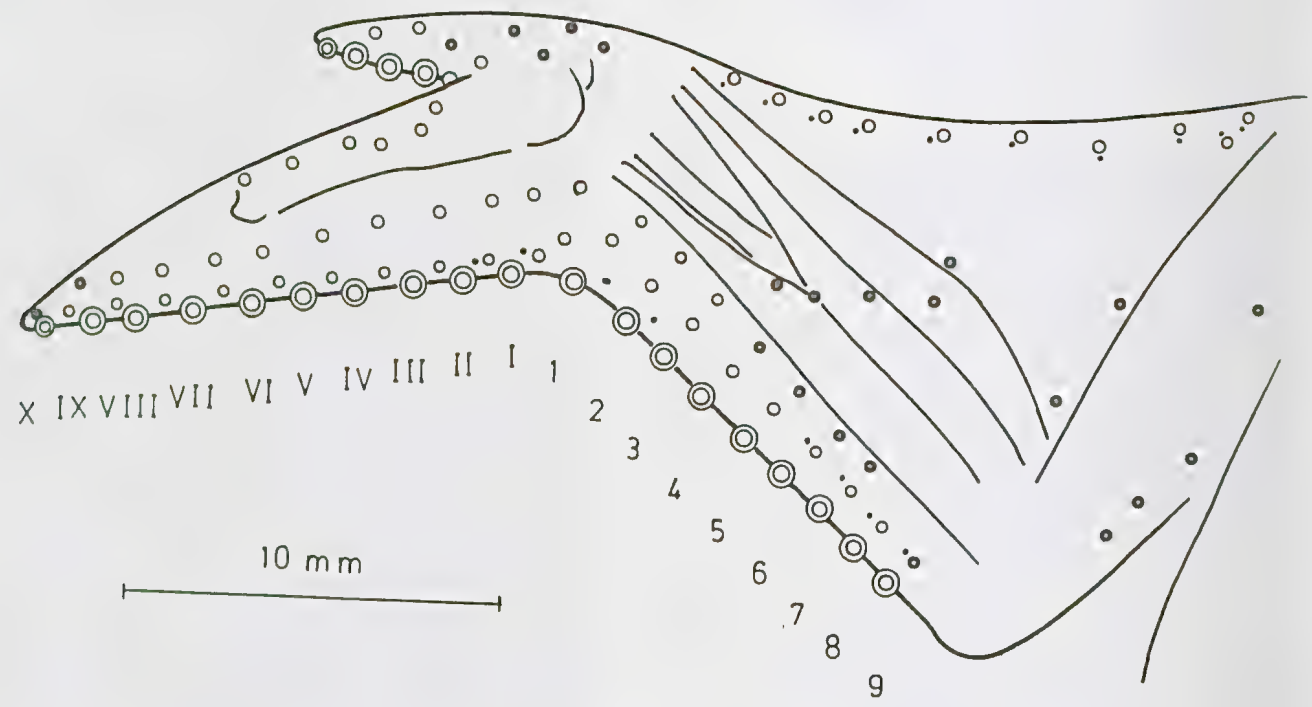

Fig. 8. Pterylosis of the wing of *Atrichornis clamosus*: ventral view.
◎ remex
o covert
• downy feather
• filoplume

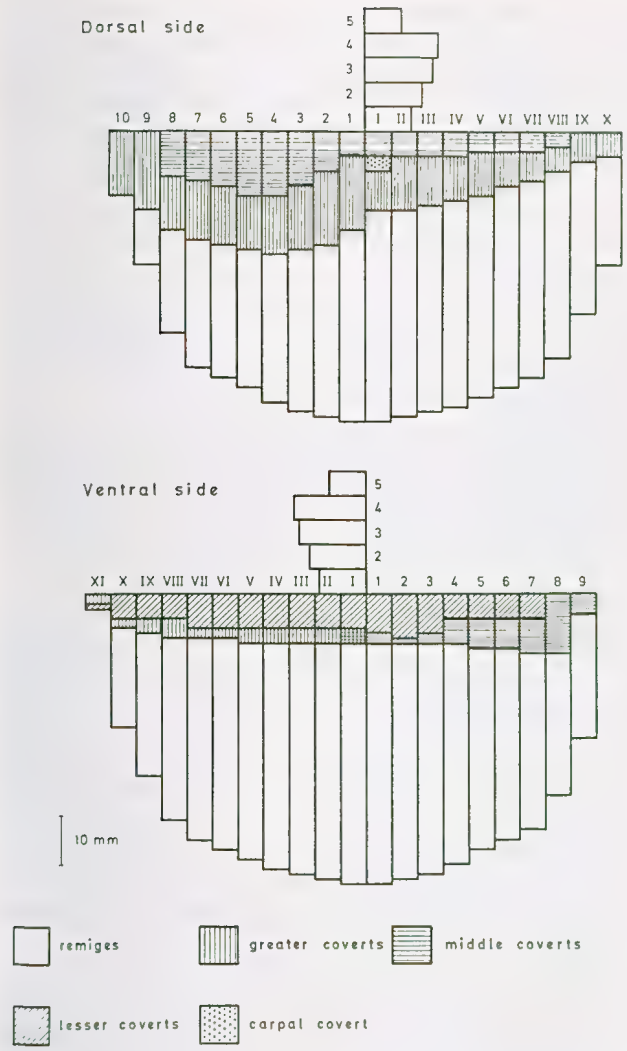

Fig. 9. *Atrichornis clamosus*: length of the principal wing feathers (the gridded area under primary I of the ventral side means both greater and middle covert presence.)

no under tertiary coverts whatsoever.

21. Alula In *Atrichornis* the alula has five well developed alula quills. The first four increase in length distally; the fifth is smaller and is followed by a sixth downy feather. Another little quill, inserted proximally to this series, appears to be another alula quill, but in structure, length and possession of a hyporachis is more similar to the alula coverts. There are seven upper alula coverts with a weak, filamentous hyporachis. On the ventral side of the alula, two or three little quills and five downy feathers are present.

In *Menura* the alula has six well developed quills. Most Passeres have three or four alula quills. Distally, the alula feathers increase in length. The most distal three have the largest rachis, the proximal three have a weaker rachis. They overlap distal-over-proximal and are accompanied by downy feathers or filoplumes. On the dorsal side of the wing, each alula quill has at least one proximal covert. In total, there are three rows of alula coverts and a fourth row of downy feathers on the dorsal side of the wing. On the ventral side, some downy feathers are irregularly scattered all over the alula surface.

22. Carpal remex and carpal covert. No carpal remex is found in *Atrichornis*. At the proximal side of the first primary, a well developed carpal covert inserts. It is longer than the upper middle primary coverts. It is posterodistally directed and has a weak hyporachis. No downy feathers or filoplumes are near it.

The length of the remiges and wing coverts of *Atrichornis* is pictured in Fig. 9.

In *Menura* there is no carpal remex, but a well developed carpal covert lies in direct line with the upper greater secondary coverts, proximal to the calamus of the first primary. It is situated in the position of the first upper middle primary covert, but is distinctly larger and has a stronger rachis than do the upper primary middle coverts. There is no hyporachis.

B. Humeral tract

Figs 1, 2, 5 and 6

In its broadest part the pteryla humeralis in *Atrichornis* is composed of four parallel feather rows. Many humeral coverts, and especially those in the periphery, have a filoplume. A weak hyporachis is present. Downy feathers are not found in this pteryla.

In *Menura* this pteryla is formed by a band of feathers that lies obliquely across the upper arm. Transverse and longitudinal rows can be distinguished. The quills of the distal part have a stronger rachis than do those of the proximal part. Distally, this tract is continuous with the upper marginal coverts. A hyporachis is lacking. In the proximal area, some of the humeral feathers are accompanied by a filoplume.

C. Caudal tract

Figs 10–12, Table 2

a. Caudal region

1. Retrices. In *Atrichornis* there are six pairs of retrices. Unlike *Menura*, they are not greatly extended and specialised in structure. All of them, the central pair included, insert on the same oblique line. The rachis of the fifth and sixth pair of rectrices is much smaller than that of the other pairs. On the dorsal side, each of the central rectrices possesses three to four (7 mm long) filoplumes on the medial side. All rectrices, except the fifth and sixth, have another distal filoplume. No downy feathers are found in their vicinity. On the ventral side most rectrices have a dorsal or distal filoplume, and lack accompanying downy feathers.

In *Menura*, the tail of the male bird has eight pairs of rectrices. These sixteen feathers are inserted in a large and highly muscularised tail, which can be raised or lowered by the bird at will. The rectrices are usually carried extended behind the bird's body in the normal

fashion, but during display they are raised and held over and parallel to the back while being vibrated (Smith, 1965).

The first, or central pair of rectrices are generally referred to as the medians or 'wires'. These rectrices are very narrow and practically devoid of vane. The inner side carries very short, widely spaced barbs; the outer side has a very narrow vane which gradually increases in width from the proximal to the distal end of the feather, until it reaches 10 mm in width. Proximally, the diameter of the rachis is 3 mm but at the tip it is nearly as thin as the barbs themselves.

The next six pairs of rectrices, or filamentaries, consist of a central shaft of 4 mm diameter, which tapers toward the extremity with numerous barbs on either side. In the proximal portion these filamentaries have barbs with interlocking barbules, resulting in a continuous vanelike appearance. This vane is longest and widest in the central filamentaries, gradually decreasing in the side filamentaries.

The eighth pair of rectrices, or lyrates, have the thickest rachis. On the inner side of these quills, there is a small vane of short and stiff barbs; the inner vane gradually increases in width from the proximal end (6 mm) to the distal tip (18 mm). On the outer side, the vane is formed by fine and flexible barbs and exhibits a number of V-shaped transparent windows. This effect is produced by the absence of barbules in the V-shaped areas (Smith, 1965). All the rectrices, even the central pair, insert on the same oblique line.

On the dorsal side of the tail, each rectrix of the first pair is surrounded by five minuscule feathers (3–4 mm in length) with a distinct rachis and hyporachis. Rectrices 2 through 7 have two accompanying distal tiny feathers, and sometimes a very short filoplume. The eighth pair of rectrices is accompanied by two downy feathers. A few more small feathers are scattered in the space above the first pair of rectrices.

On the ventral side, a series of minuscule quills is present between the first rectrices. Each rectrix itself is surrounded by three tiny feathers and all the other rectrices, except the last pair, are generally accompanied by at least two minuscule feathers, the inferior one being the smallest and more downy. The eighth rectrix has one or two distal downy feathers.

2. Greater upper tail coverts. In *Atrichornis*, five pairs of greater upper tail coverts are present. Pair 1 apparently is missing, but on the left side (only) a very small and weak covert is inserted at the same level as the second greater upper tail covert. The second, third and fourth greater upper tail coverts lie over the middle of the corresponding rectrix; the fifth and sixth lie on the proximal side of their rectrix. All coverts lie parallel to their rectrices. Their barbs converge medially and a filamentous hyporachis is seen. No downy feathers or filoplumes accompany these coverts.

Eight pairs of greater upper tail coverts are present in *Menura*. Each tail covert bears the same number as its corresponding rectrix. Pair 1 is missing. Pair 2 lies on the distal side of its rectrix; pairs 3–5 lie on the medial side. The ninth greater upper tail covert is very weak and lies close to the eighth, over the middle of the eighth rectrix. The rachis of the seventh and eighth pair of coverts is smaller than those of the other coverts. The rachis of the ninth is substantially smaller.

A very small pennaceous feather inserts medially to pair 2 of the greater upper tail coverts. The other coverts have an accompanying downy feather or, more commonly, a filoplume. On the right side between and above the seventh and eighth greater upper tail coverts, and on the left side between and above the eighth and ninth greater upper tail coverts, another small pennaceous feather is present.

3. Lesser upper tail covert. In *Atrichornis* one pair of lesser upper tail coverts is present. They insert mediodorsally to the first pair of rectrices. They possess a very weak hyporachis. No downy feathers or filoplumes are found near them. The lesser upper tail coverts are completely missing in *Menura*.

4. Greater under tail coverts. On the ventral side there are at least five pairs of greater under tail coverts in *Atrichornis*. The sixth pair was missing in this specimen, but as the ventral side of the tail was slightly damaged we may not exclude the presence of an outermost pair of coverts. The first three coverts insert on the distal side of their rectrix, the fourth and fifth on the medial side. All have a rather weak hyporachis. Only the first pair of coverts has a medial filoplume. Halfway between the insertion of the first rectrix and its greater under tail covert, another filoplume originates from an obvious papilla.

On the ventral side there are eight pairs of greater under tail coverts in *Menura*. This row runs parallel to that of the rectrices. Pair 1 is missing; pairs 2–4 are situated on the middle of their corresponding rectrix; pairs 5–7 lie on the medial side of their rectrix; pair 8 is on the distal side of the seventh rectrix; and pair 9 lies on the medial side of the eighth rectrix. Most of the coverts are accompanied by a very short filoplume. Sometimes a supplementary downy feather or minuscule pennaceous feather can be found near the medial ones.

5. Lesser under tail coverts. In *Atrichornis* only the first pair of lesser under tail coverts is present. It inserts between the first and second rectrix, bare anterodistally to the first greater under tail covert. It has a weak hyporachis. The length of the rectrices and tail coverts of *Atrichornis* is pictured in Fig. 12.

The lesser under tail coverts are missing in *Menura*.

b. Uropygial region

In *Atrichornis*, the papilla of the bilobate oil gland is bare but the body of the gland has an irregular scattering of weak, downy pennaceous feathers with a weak hyporachis.

In *Menura*, the papilla of the bilobate oil gland is devoid of feathers; even the feather tuft encircling the orifices is missing. Downy feathers and very small

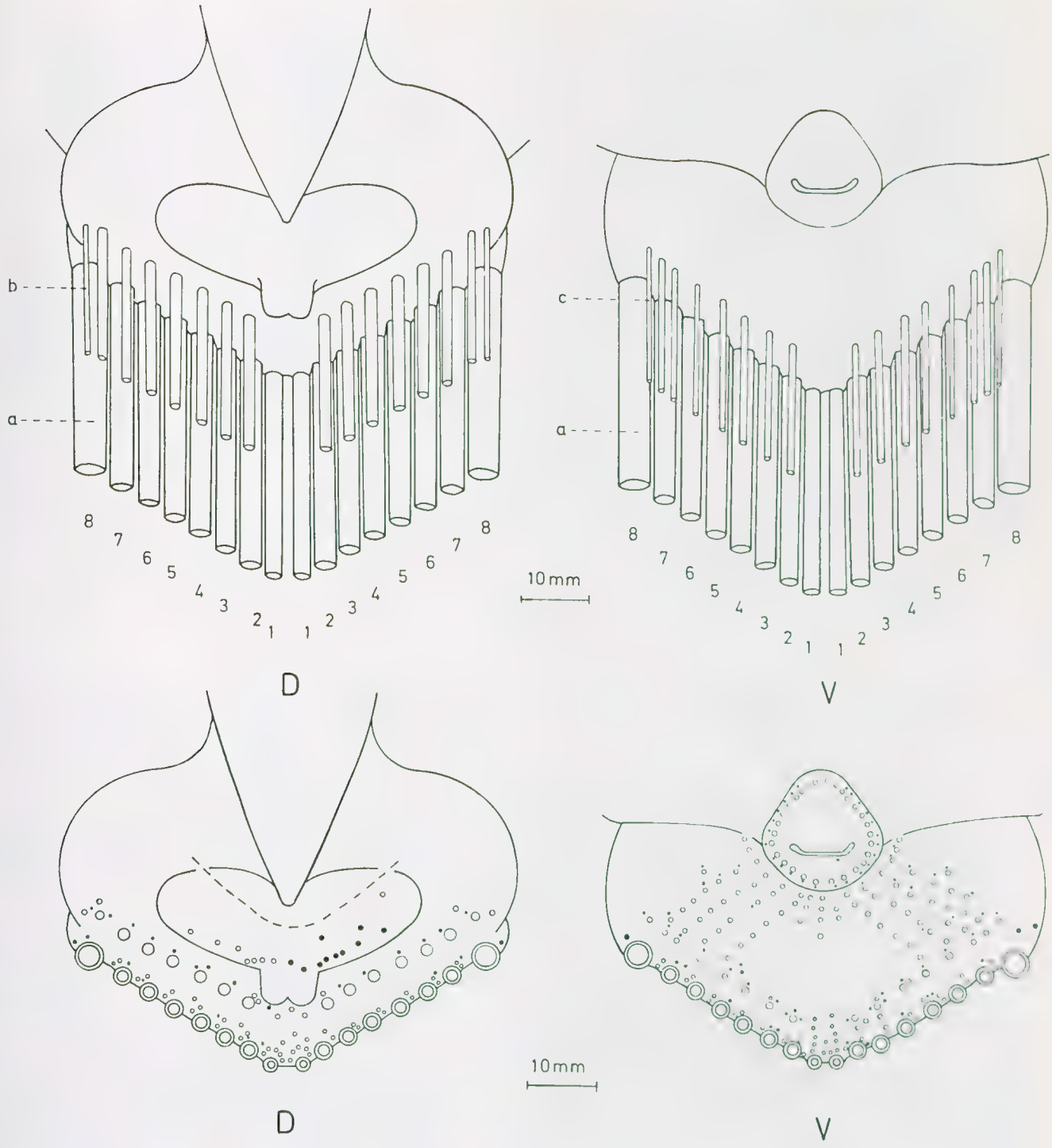

Fig. 10. *Menura novaehollandiae*: caudal tract.
D. dorsal side
V. ventral side
a. rectrices
b. greater upper tail coverts
c. greater under tail coverts

◎ rectrix
o covert
• downy feather
• filoplume

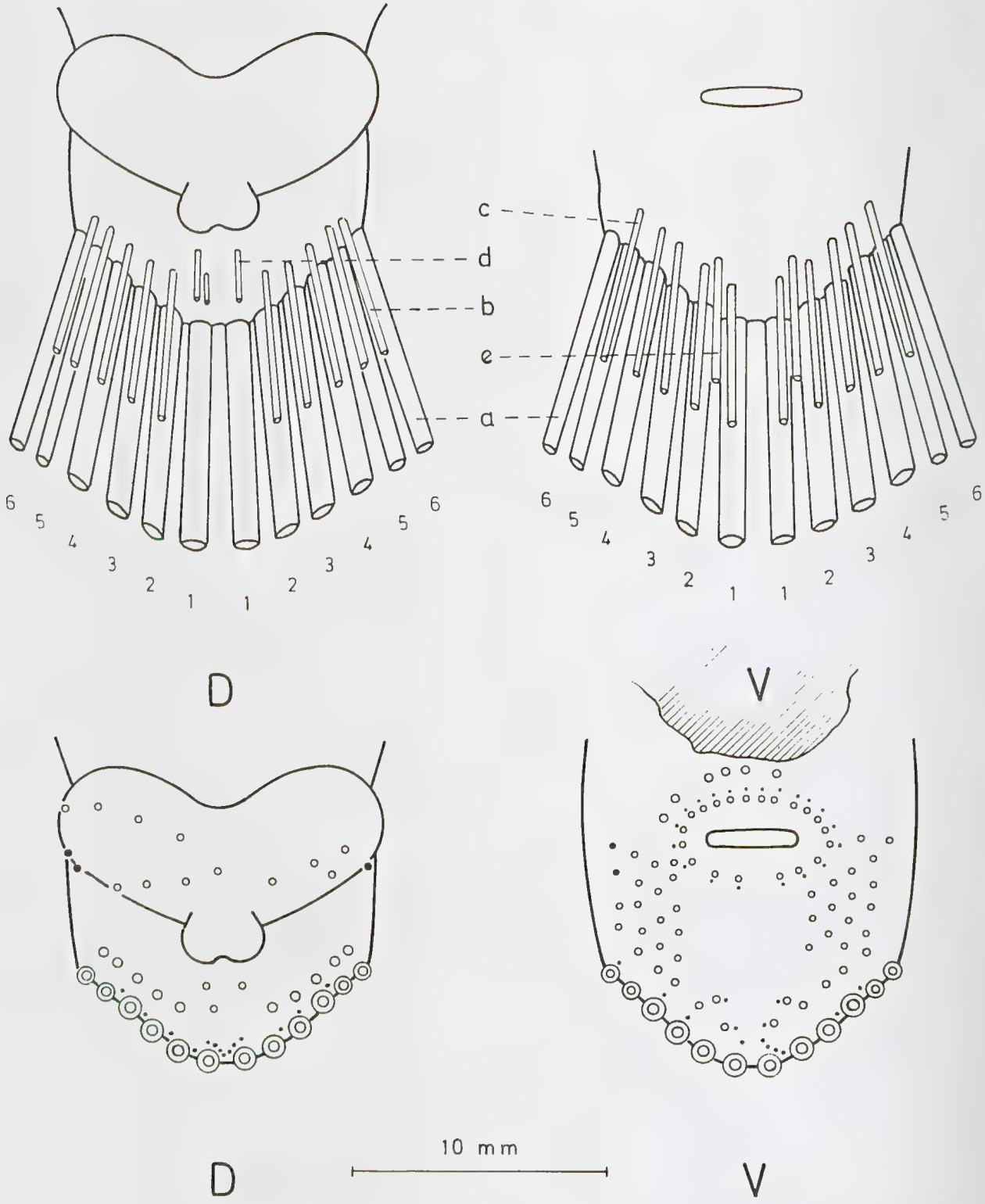

Fig. 11. *Atrichornis clamosus*: caudal tract.
D. dorsal side
V. ventral side
a. retrices
b. greater upper tail coverts
d. lesser upper tail coverts
c. greater under tail coverts
e. lesser under tail coverts

◎ rectrix
o covert
◉ downy feather
• filoplume

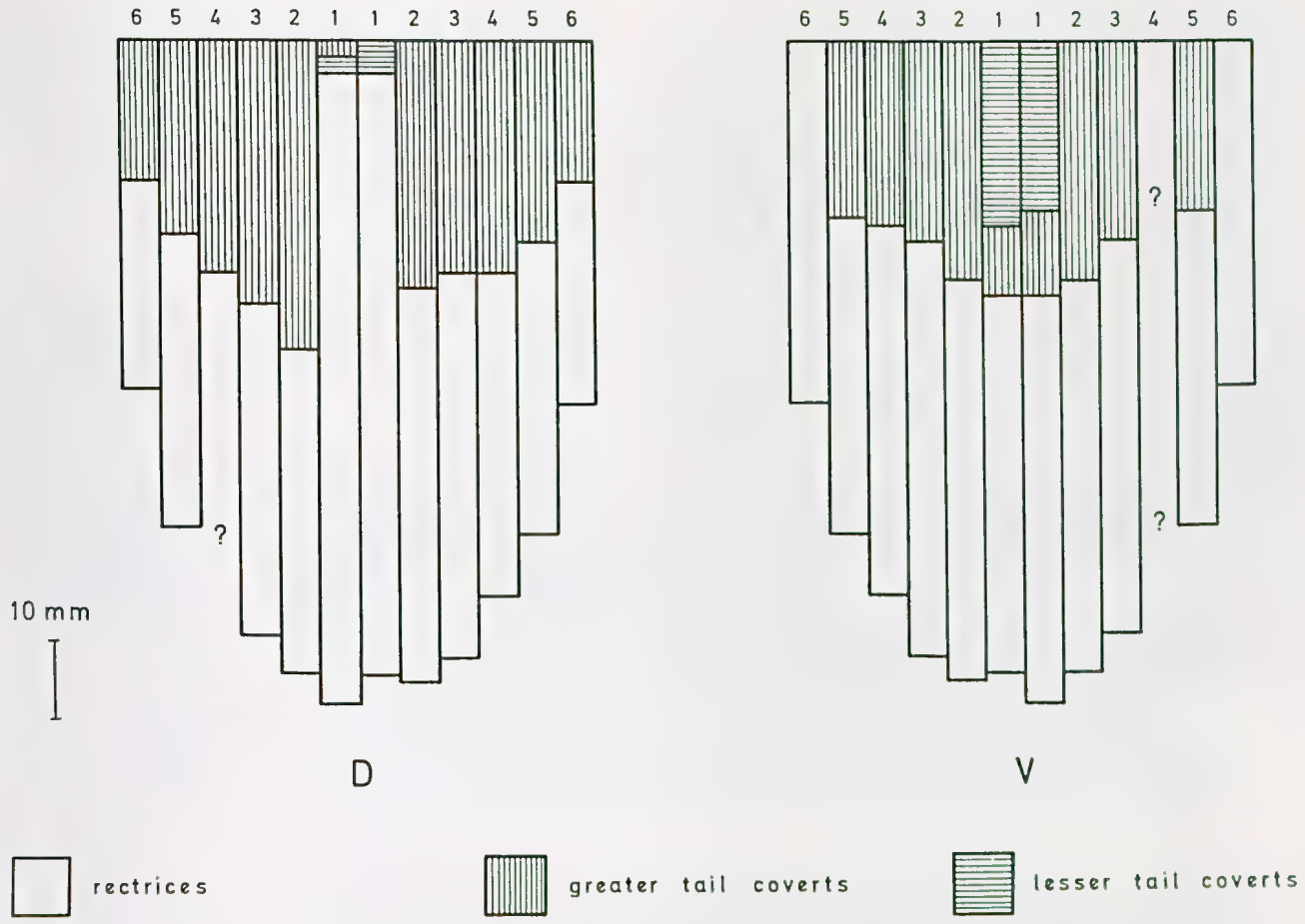

Fig. 12. *Atrichornis clamosus*: length of the principal tail feathers.
D. dorsal side V. ventral side

pennaceous feathers are scattered along the posterior border of the gland.

c. Postpelvic region

A few downy feathers are found in the postpelvic region in *Atrichornis* but in *Menura* this region is naked.

d. Anal region

The anal region was slightly damaged in the specimen of *Atrichornis*. A caudally open circumanal ring surrounds the anus. In the cranial half of the ring the length of the feathers decreases from distal to medial; in the caudal half the feathers are all nearly the same length. They have a weak hyporachis. Their accompanying filoplumes, inserted on obvious papillae, form another, outer circle. Cranially, six other coverts form an incomplete semicircle of feathers.

In *Menura* the anal region is ringed by a complete circle of 28 small contour feathers without a hyporachis. Accompanying filoplumes insert near the coverts and form a supplementary outer circle. Only the most cranial coverts lack a filoplume. The length of the feathers increases from the middle of the cranial (5 mm) and caudal halves (9 mm) toward the more distal margins (27 mm). Caudal to the feather circle, some downy feathers form a second feather arch (not visible) in the Fig. 10).

e. Postventral region

In *Atrichornis* the postventral region consists of two separated groups of feathers. These feathers have a weak hyporachis and filoplumes are scarce.

In *Menura* the two parts of the postventral region converge medially and join each other under the anal region. These coverts lack a hyporachis and some of them, especially in the peripherical part, are accompanied by a filoplume.

CONCLUSION

On comparing the wing pterylosis of *Atrichornis clamosus* and *Menura novaehollandiae* a great difference can be seen in the number of the remiges and coverts, especially those on the forearm. Striking features are the presence of eleven primaries in *Menura* (ten in *Atrichornis*) as well as the presence of a series of primary upper lesser secondary coverts (absent in

Atrichornis). Another remarkable point is the great number of secondaries (14) and corresponding coverts present in *Menura*. In comparison with *Ploceus nigerrimus* (Morlion, 1971), chosen as a representative passerine, we see that in wing pterylosis *Atrichornis* is much nearer to the Passeres than is *Menura*. There are fewer differences in wing pterylosis between *Atrichornis* and *Ploceus* than between *Atrichornis* and *Menura*.

In the tail pterylosis a great difference also exists between the two species investigated: not only in the aspect of the feathers, but also in the numbers of rectrices, greater upper and under tail coverts, and in the presence or absence of the first pair of upper and under tail coverts. In contrast to the wing pterylosis, however, the tail pterylosis of *Atrichornis* is markedly different from *Ploceus nigerrimus* in the presence of the first pair of lesser upper tail coverts and in the possession of only five pairs of greater under tail coverts.

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Alula quills												9	11	13	14	7						
Upper lesser coverts	–	–	–	☆	☆	☆	☆	☆	☆	☆		–	–	–	–	–	–	–	–	–	–	
Upper middle coverts	–	–	9	10	11	13	13	11	8	5	–	5	5	5	5	4	4	4	3	–	–	
Upper greater coverts	13	16	20	22	23	24	25	24	23	20	8	16	16	15	14	13	11	10	8	6	5	
Remiges	–	27	41	48	50	52	55	57	58	59	–	59	58	57	56	54	52	50	46	37	27	
Number	10	9	8	7	6	5	4	3	2	1	C	I	II	III	IV	V	VI	VII	VIII	IX	X	
Under greater coverts	–	–	–	–	–	–	–	–	–	–	–	10	10	10	10	10	9	9	9	8	7	2
Under middle coverts	–	4	12	12	11	11	10	10	10	10		10	–	–	–	–	–	–	–	–	–	–
Under lesser coverts	–	–	–	5	5	5	5	8	9	8		7	7	7	7	7	7	7	5	5	5	3

Roman numerals : primaries and primary coverts.
Arabic numerals : secondaries and secondary coverts.
C : carpus (carpal coverts / carpal remex)
Underlined numbers : length of downy feathers.
☆ : downy feathers not measured.

Table 1. Measurements of the principal wing feathers of *Atrichornis clamosus* (in mm).

Lesser upper tail coverts	–	–	–	–	–	4	4	–	–	–	–	–
Greater upper tail coverts	18	25	30	34	40	2	?	32	30	30	26	18
Rectrices	45	63	?	77	82	86	82	83	80	72	64	47
Number	6	5	4	3	2	1	1	2	3	4	5	6
Greater under tail converts	–	22	?	26	31	33	33	31	26	24	23	–
Lesser under tail coverts	–	–	–	–	–	22	24	–	–	–	–	–

Underlined number: length of a downy feather.
?: missing feather

Table 2. Measurements of the principal tail feathers of *Atrichornis clamosus* (in mm).

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Natal Downs and Plumage Changes in the Noisy Scrub-bird, *Atrichornis clamosus* (Passeriformes: Atrichornithidae)

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ABSTRACT. The newly hatched Noisy Scrub-bird chick has 60 to 81 natal downs distributed in three paired and two single dorsal pterylae. The downs are most numerous and longest on the capital and spinal tracts. The age of the chicks when the contour feather sheaths emerge and burst on the various regions of the body is described. Males and females show no differences in the natal downs or juvenal plumage. The first moult begins when the chick is 41 to 46 days old. The first basic plumage is like the adult female plumage except that the male has a faint grey pectoral band on the upper chest. The second moult takes place during the bird's second summer, through which it attains the second basic (definitive) plumage. The males differ mainly in having a black upper pectoral band. All plumages are described. The distribution of the 840 natal downs in five paired and four single pterylae (both dorsal and ventral) in one specimen of the Superb Lyrebird is described. The differences in the natal downs and subsequent plumages between the scrub-birds and lyrebirds are discussed.

SMITH, G.T., 1978. Natal downs and plumage changes in the Noisy Scrub-bird, *Atrichornis clamosus* (Passeriformes: Atrichornithidae). Records of the Australian Museum 37(3): 157–163.

KEYWORDS: Atrichornithidae, Menuridae, moult, natal downs, plumage changes.

Of the Nosiy Scrub-birds (*Atrichornis clamosus*) collected in the period 1842–1889 (Whittell, 1943; Mees, 1964), only 20 specimens have survived. All were thought to be males until Campbell (1939) described a specimen from the Museum of Victoria that he considered to be a female. This was confirmed when Whittell (1942) published a description of a hitherto overlooked female in the collection of the Academy of Natural Sciences in Philadelphia. The only other published information on Noisy Scrub-bird plumages is a description of a male in first basic plumage (Serventy, 1967) and a brief description of the juvenal plumage (under the heading 'immature') by Smith (1976a). Only brief descriptions of the natal downs are available for the Rufous Scrub-bird (*A. rufescens*) (Jackson, 1921) and Superb Lyrebird (*Menura novaehollandiae*) (Kitson, 1905; Tregallas, 1921; Leach, 1921; Reilly, 1970). Those of the Albert Lyrebird (*M.alberti*) have not been recorded.

The present article describes, for the Noisy Scrub-bird, the distribution and numbers of natal downs per pteryla, the feather development of nestlings, and plumage changes from fledging to maturity. The natal down from one Superb Lyrebird is also described. The aim is to present another body of data that may help to elucidate the relationships of the Menurae.

METHODS

The description of the natal down was based on two wild Noisy Scrub-bird nestlings that died at age one and five days respectively, and one six day old nestling hatched in captivity from an egg collected in the wild. An embryo approximately two to four days from hatching was examined also (the incubation period is 36–38 days; Smith & Robertson, 1976). These data were supplemented by descriptions and photographs of newly hatched chicks in the wild. For each specimen, the number of natal downs in each pteryla was counted and, for the three chicks, the length of five downs on each pteryla measured. All downs were measured in pterylae with five or fewer downs. The number of barbs in a representative sample of downs was counted. Neossoptile terminology is that of Wetherbee (1957).

Descriptions of the feather growth in the nestlings are based on descriptions from 31 individuals in the wild. The number of observations per chick ranged from one to seven, depending on the stage at which the nest was

found. Nests could only be visited once after the nestling was about 16 days old because of the risk that the chick might leave the nest prematurely. The main reason for handling the nestlings was to obtain growth data that could be used to determine age. If the female was near the nest and appeared agitated, only brief notes were made. Because of these limitations, no complete sequence of descriptions was obtained from any one bird. As a result, the descriptions presented here are a composite from all individuals.

Plumage changes after fledging were documented from three females and one male held in captivity. They were acquired as nestlings when 16–19 days old and maintained in a cage, made from a tea chest, until 80–120 days old. Then they were placed in a small aviary (2 × 2 × 3.5 m) and later transferred to a larger one (25 × 8 m).

They were only handled twice in the small aviary and not at all while in the larger aviary. One female bird bred in captivity was examined briefly when four months old and again when 16 months old (Smith *et al.*, 1983). The natal downs from a four-to-six-day-old Superb Lyrebird were also examined.

RESULTS

Natal Down

At hatching, the chick is blind, weighs four to five grams and is 40–50 mm in length. A dense line of grey down runs from the crown to the rump, with small thin patches on the shoulders and thighs (Fig. 1). There are eight pterylae distributed as shown in Fig. 2. Both sides of the paired coronal, scapular and femoral tracts are individually numbered 1–2, 4–5 and 7–8 respectively. The number of downs on the two sides are usually not equal as is often the case in passerines (Wetherby, 1957). The natal downs have a short calamus with 7 to 15 barbs and no rachis; each barb has many plumulaceous barbules.

The number and average lengths of the downs in each pteryla are given in Table 1. The occipital (number 3) and spinal (6) pterylae have more and longer down than the other pterylae, although the down in the coronal (superciliary) tract (1,2) is almost as long. The down in the other tracts is shorter and more widely spaced. Observations on wild, newly hatched nestlings indicate that the distribution, number and length of downs found

Fig. 1. Noisy Scrub-bird chick, one to two days old.

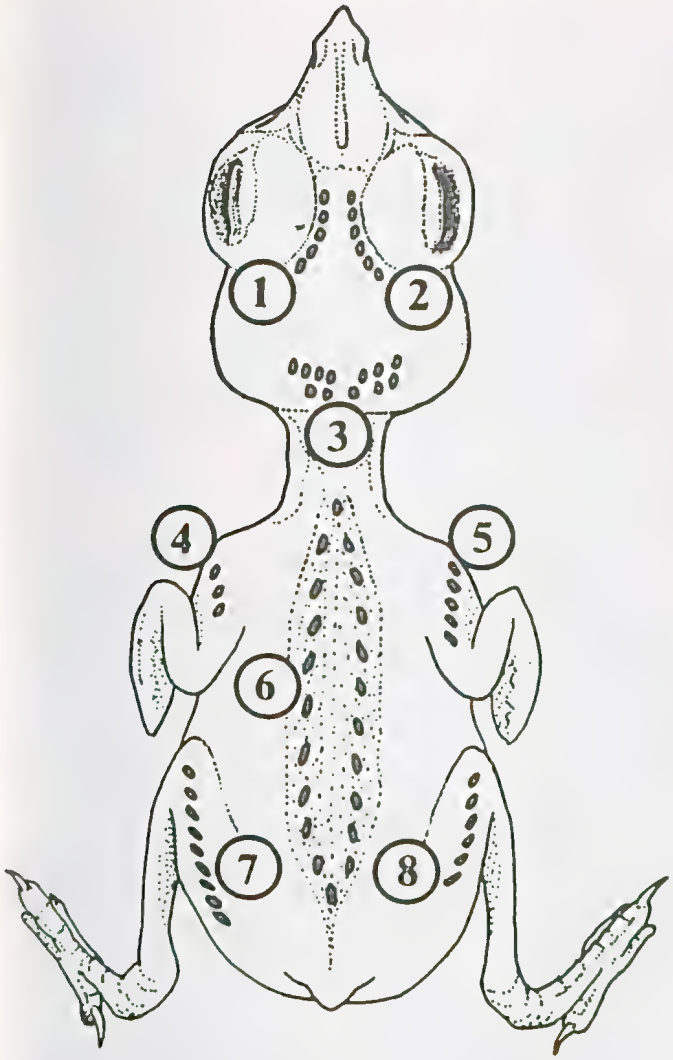

Fig. 2. Distribution of downs in the eight pterylae of the Noisy Scrub-bird chick (drawn from Bird 1).

on the specimens studied was within the range of that of wild, healthy birds. Photographs suggest some variation in the number and length of downs and that Birds 1 and 2 were probably at the lower end of the range, as one might expect from nestlings that died shortly after hatching. Bird 3 appeared to be average, its early death being related to the aviary conditions. The data in Table 1 show that variation in the amount of down may result from differences in the number and length of downs as well as from the number of barbs in each down.

The spinal tract is a distinctive grey weal caused by the prominence of barbed follicles; each down feather in this tract has its calamus surrounded by a sheath of barbs from the first generation of contour feathers.

Development of Juvenal Plumage

Feathers. The ages at which the contour feather sheaths emerge and burst on various regions of the body are shown in Fig. 3. The data are pooled from 31 chicks. Only six of the chicks were subsequently sexed (five females, one male) and an additional four chicks were tentatively sexed as males on their growth characteristics. Examination of the data from these chicks suggests that there is no significant difference between the sexes in the development of plumage.

As is typical of passerines, the first generation of contour feathers is more loosely textured than are the later generations. The first feather sheaths to emerge are those on the spinal tract at the second day after hatching (D2); by D6 the sheaths in all tracts have started to emerge, except those on the chin which do not start until D9. Within each tract there is considerable variation in the age at which individual feather sheaths emerge. Fig. 3 gives the age when the first sheaths emerge in the various pterylae. The difference among individuals in the age at which the sheaths burst is three to eight days.

In general, the sheaths burst first on the trunk, while those on the head and appendages break open later. The

	BIRD 1 (5 day old)			BIRD 2 (1 day old)			BIRD 3 (6 day old)			BIRD 4 (32-34-day-old embryo)		
Feather Tract	No. Downs	Mean Down L. (range)	No. Barbs	No. Downs	Mean Down L. (range)	No. Barbs	No. Downs	Mean Down L. (range)	No. Barbs	No. Downs	Down L.	No. Barbs
1	5	16 (15–17)	–	5	16 (12–18)	–	8	16 (15–17)	–	7	18	–
2	6	16 (15–18)	11	6	18 (17–18)	–	8	16 (15–18)	13	8	15	–
3	12	21 (18–22)	15	18	24 (22–28)	10	26	21 (17–22)	15	13	26	–
4	3	11 (9–12)	–	4	13 (12–14)	7	5	10 (9–10)	–	*	*	–
5	5	12 (11–15)	–	2	10	–	7	13 (10–16)	–	4	11	–
6	21	19 (8–20)	12	20	18 (16–19)	10	18	20 (17–25)	10	7	18	–
7	9	10 (8–13)	–	6	15 (12–16)	10	11	12 (11–15)	–	9	13	–
8	6	12 (11–13)	–	6	–	–	8	13 (11–15)	–	9	15	–

* no down; – not counted

Table 1. Number and mean length (mm) of natal downs in the pterylae (see Fig. 1), and the number of barbs in a single natal down from some pterylae of 3 nestling *Atrichornis clamosus*. Only the number of downs and the length of an average down were counted in Bird 4 (a late embryo).

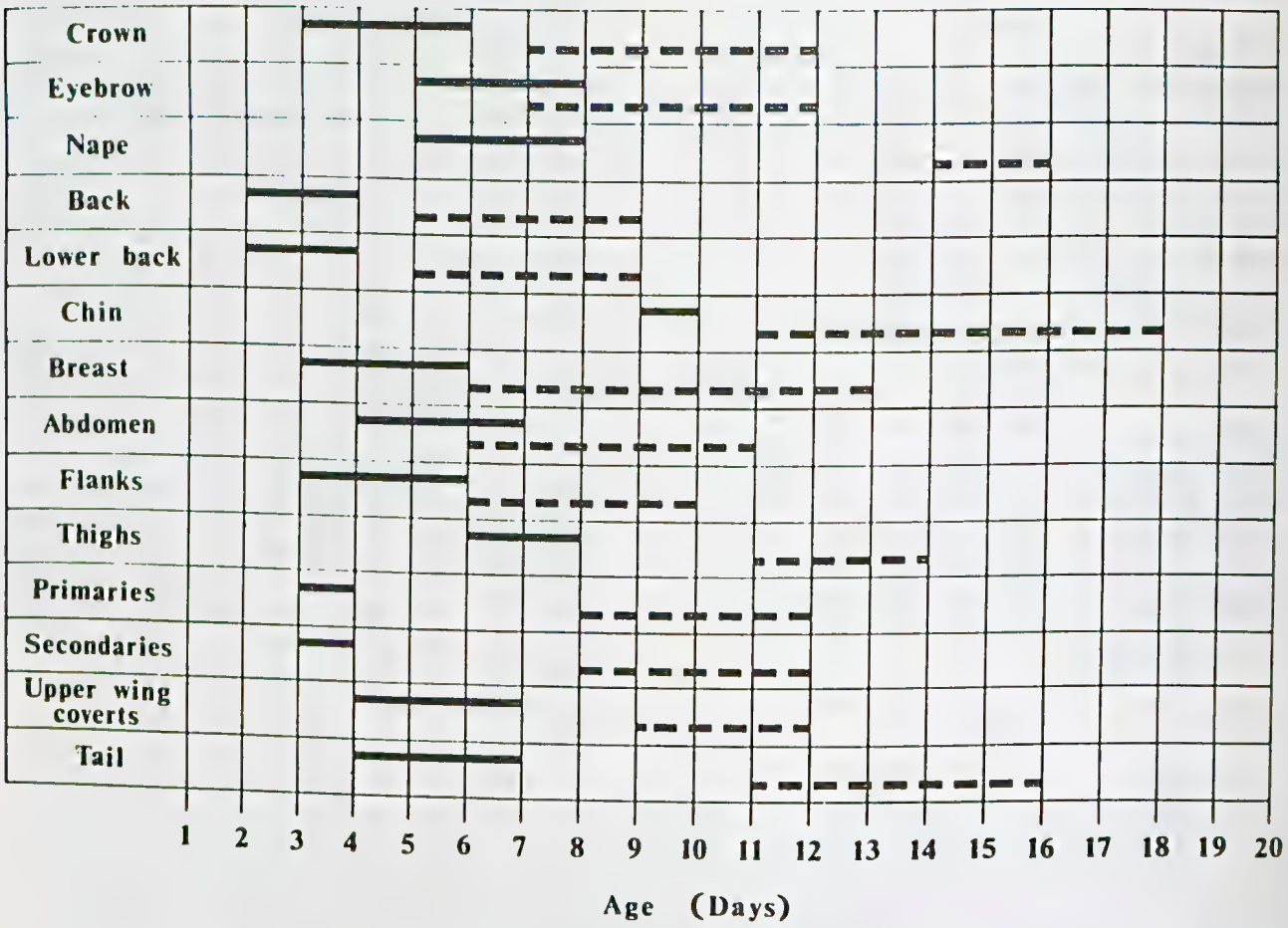

Fig. 3. Range of ages when the feather sheaths first emerge (solid line) and burst (dashed line) on various regions of the Noisy Scrub-bird nestling.

majority of sheaths have started to burst by D18. By the time of fledging (D21–28), the chicks are well feathered, with only a few traces of down and a short tail (25–40mm); at fledging, some feather sheaths still have not burst in the superciliary region, forehead and chin.

Soft parts. The eyes are closed until D3–4 and the eyes of all birds are fully open by D9–12. The eye colour is dark brown, as in the adults.

The colour of the gape at hatching varies from cream (N = 4), pale yellow (N = 6), to yellow (N = 2). By D21 the colour has deepened and ranges from pale yellow (N = 1), yellow (N = 14), to deep yellow (N = 2). Data from nine individuals confirm this progressive deepening of the colour in birds that are hatched with pale gapes. Two birds with yellow gapes at hatching showed no change. At hatching, the mouth is pink and by D4 it has a yellow tinge. At D21 it ranges from pinkish yellow to yellow.

The bill at hatching is pink; by D3 the maxilla has a touch of grey and by D8 it is a dark grey-brown. The mandible may change slowly from pink to cream with a dark proximal end, or it may stay pink until fledging.

The legs are pink at hatching and by D8 have started to go grey; by D21 they are dark grey-brown as in adults. There were no apparent differences in the development or colour of the soft parts between the sexes.

The egg tooth is present until D7 and in all chicks it has been shed between D9 and D14.

Juvenal plumage. There is no apparent difference between the sexes in this plumage. By about D30 the feather sheaths on the superciliary region, forehead and chin have all burst and the bird appears fully feathered except for the short, still-growing tail which is not fully grown until the bird is about 70 days old.

The following description is based on the four captive birds and those found in the wild before fledging: head, nape and mantle cinnamon-brown, darker on the nape and sides of the head; superciliary cream; lower back, upper tail coverts and crissum of dense, grey, loosely textured feathers; throat and breast cinnamon, lighter on throat and grading to grey on the flanks; abdomen grey, tipped with pale cinnamon to give a scalloped effect; thighs chestnut grading to grey; there is a circle of chestnut feathers above the knee.

Primaries and secondaries chestnut on the leading side

of the rachis and grey on the trailing side; tail grey and not completely grown; eye dark brown; gape yellow; maxilla grey-brown; mandible flesh-cream; legs dark grey-brown.

First prebasic moult. Only body feathers are replaced in the first moult. Two females and the male in captivity began the first prebasic moult at 41, 46 and 41 days old, respectively, and finished 49, 55 and 79 days later. The exact time and duration of the moult for the third female was not recorded, but it was similar to that of the other females. Thus the females moulted faster than the male, completing the moult in about 50 days. The more protracted moult of the male, moreover, rarely looked heavy. The sequence of moulting in the various parts of the body was similar to that found in the eruption of the juvenal plumage.

First Basic Plumage

Male. Head, nape and mantle rich brown with darker crossbars, superciliary cream; lower back and upper tail coverts dark grey; chin and throat cream-white grading to grey-buff on the chest, and grey tipped with buff on the flanks; crissum dark grey; faint grey line across upper chest; tail grey with cross bars on the proximal quarter; wing and soft parts as for the juvenal plumage.

Female. Similar to male, but without the faint grey line across the upper breast.

Discussion. The main differences between the juvenal and first basic plumages are that (1) the loosely textured feathers on the lower back and around the vent are replaced by normally textured contour feathers, (2) the colour of the head, nape and mantle changes from cinnamon-brown to rich brown with darker crossbars, and (3) the still-growing tail becomes barred basally.

Second prebasic moult. This takes place during the birds' second summer, during the period from late October to March. Like the males' first prebasic moult, it is a slow and gradual process. Scrub-birds at this stage are shy and retiring, but none were seen in heavy moult.

Second Basic (Definitive) Plumage

With the second prebasic moult, both the males and females acquire 'adult' plumage.

Male. As for the first basic plumage, but the chin and throat are white and subtended by a definite black upper pectoral band which widens to the midline to extend slightly upward to the chin and down toward the belly. The crissum is rufous and the rump brown-grey with darker bands.

Female. As for the male but the chin and throat are cream, grading to pale buff on the chest; there is no black pectoral band. The crissum may be grey, tipped with cinnamon or rufous. In one of the captive females the vent became rufous after the third moult. Females in the wild also appear to vary in vent colour after the second moult.

Superb Lyrebird

The distribution of natal down is shown in Fig. 4 and the number of downs in each tract and the range of the length of downs in some of the tracts are listed in Table 2. In lyrebirds, down occurs in more tracts than it does in scrub-birds; it is denser and longer in the capital and spinal tracts than elsewhere, although in tract 12 (ventral cervical) the downs are as dense even if shorter. The downs have 10–15 barbs, each of which bears short barbules. The barbules are shorter and more closely spaced than are those of the Noisy Scrub-bird.

Tract No. (Fig. 4)	No. Downs	Range of Down Length	No. Barbs
1	210	10–30	12
2	51	12–20	11
3	23	10–22	
4	22		
5	47		
6	190	21–31	12
7	25	4–7	
8	51	10–20	
9	47		
10	30		
11	34	12–18	
12	110	9–12	14
13	*		
14	*	2–7	

* not counted (badly damaged from skinning)

Table 2. Number of natal downs and the range in down length (mm) in the pterylae of a four- to six-day-old *Menura novaehollandiae* chick. The number of barbs in a single down from four pterylae is also given.

DISCUSSION

For the closely related Rufous Scrub-bird the only available information on natal downs and subsequent plumage changes are the brief descriptions by Jackson (1921) of a newly hatched chick and of three young birds aged at about three, five and eight weeks. Of the newly hatched nestling Jackson reported: "it had only a little blackish down on the head and down the middle of the back, the other portions being naked and whitish in colour". (The three juveniles in the Museum of Victoria, H.L. White collection, could not be examined.)

This brief description suggests that the length and/or number of the downs on the capital and spinal pterylae are less than those in the Noisy Scrub-bird, and further, that there are no humeral or femoral pterylae. The three-week-old bird, which from its measurements would have fledged recently, is described as being "pale reddish brown all over". This juvenal plumage is, thus, like that found in the Noisy Scrub-bird. Jackson did not give detailed plumage descriptions of the two older male birds but his general comments, noting the absence of a black bar on the chest, suggest that they had been through a first prebasic moult and that their first basic plumage is similar to that of adult females.

The natal down of the newly hatched Superb Lyrebird has been described as short and black and restricted to the head and back, the rest of the body being naked (Kitson, 1905; Reilly, 1970). Leach (1929), however, describes the nestling as being "clad in long, dark grey down" and a week-old chick is covered with thick, grey

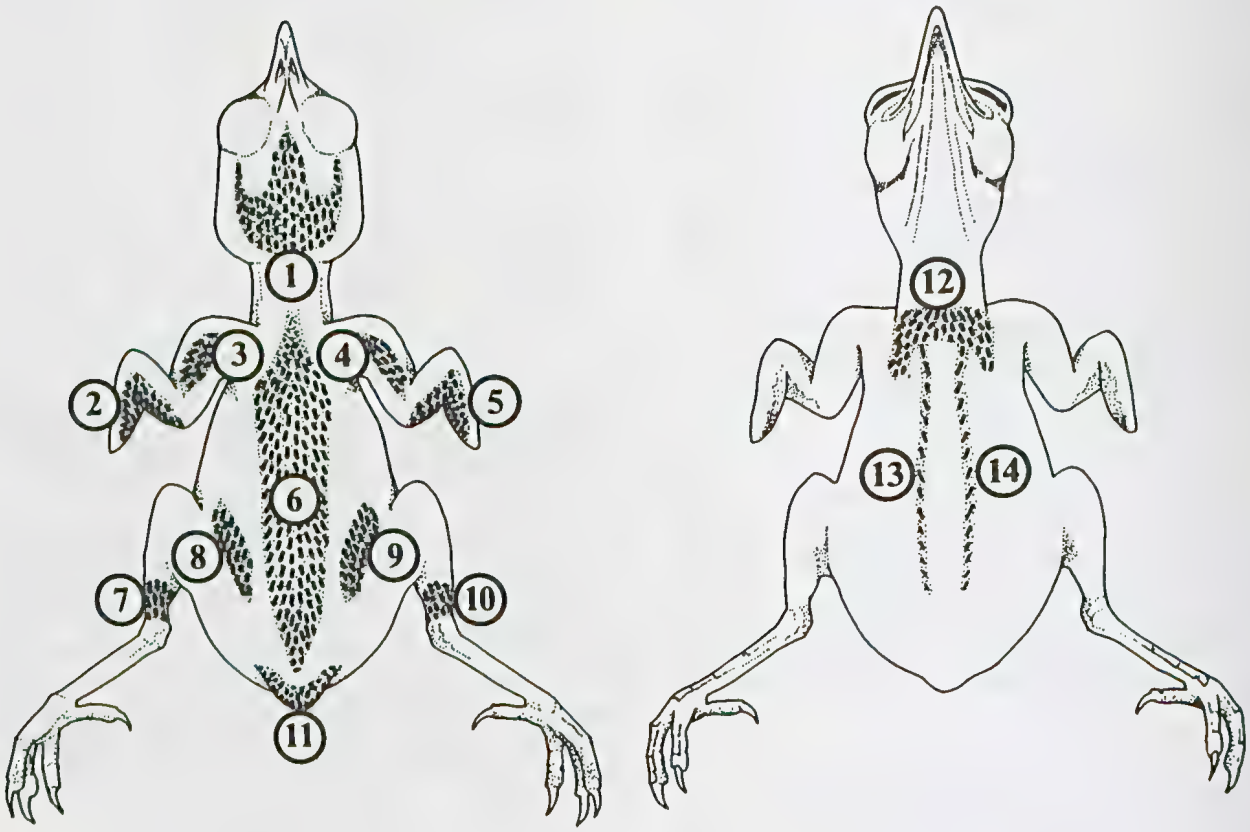

Fig. 4. Distribution of the downs on a four- to six-day-old Superb Lyrebird chick. Left, dorsal view. Right, ventral view.

down according to Tregellas (1921). A photograph of a one-day-old Superb Lyrebird nestling supplied by F.N. Robinson, and another of a very young nestling published by Thomson (1935), show the same distribution I have already described from a four to six-day-old nestling.

At fledging (about six weeks after hatching) the male Superb Lyrebird's plumage is similar to that of the adult female except for rufous tonings to the wings, back and tail coverts, and rufous patches on the forehead, chin and throat (Moroney, 1972). The rufous on the forehead is lost in the autumn moult, of the head and neck during the second year, while the rufous on the chin and neck gradually diminishes at three to four years of age. The tail is moulted in the first spring, and the male's tail gradually develops from the age of two until reaching its full form when the bird is five to eight years old.

Plumage changes in Albert's Lyrebird have not been studied.

There are clear-cut differences between natal down of the Superb Lyrebird and the Noisy Scrub-bird, the latter having fewer pterylae, and fewer and shorter downs in each pteryla. The Rufous Scrub-bird probably has still fewer and shorter downs. In the lyrebirds and the scrub-birds the female takes complete care of the nestling (Smith & Robinson, 1976; Smith, 1976b) and when the female leaves the nest to hunt, the nestling body temperature decreases (Lill, 1979). It may be that the differences in the downs are adaptations to the different temperature regimes during the early nestling periods. They might also reflect different phylogenies.

The juvenal plumage of both the scrub-birds and the lyrebird is brighter in overall tone than that of the adults. All the species are terrestrial, living in dense, dark, wet vegetation where the females care for their offspring for a period after fledging (Smith, 1976b). Experience with the Noisy Scrub-bird has shown that the juveniles are more easily seen than the adults. The brighter juvenal plumage may be an adaptation to help the female maintain short-distance contact with her chick. The brighter plumage may also enable the male to recognize young birds and thus prevent conflict between the male and his offspring.

The Noisy Scrub-bird undergoes a postfledging body moult (first prebasic) to acquire the first basic plumage, and a year later undergoes a second (prebasic) moult to assume adult (definitive) plumage. In the lyrebird, the sequence of moults and the attainment of adult

plumage are different and more complex. There is no postfledging moult. The first moult is in the autumn after fledging, at about six months of age, and only affects the head; the tail moults in the following spring. There are no data on the timing of the body and wing moults. Adult plumage is not acquired by the females until three or four years of age, and by the males not until five to seven years. Such a time span has closer parallels in the Ptilonorhynchidae (bower-birds) and Paradisaeidae (birds-of-paradise) (Sibley, 1974).

The large differences in the number and distribution of the natal downs and the plumage development between the scrub-birds and lyrebirds suggest that the two families are not closely related. Further studies on related families need to be done before the taxonomic significance (if any) of the recorded differences can be established.

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Osteological Comparison of the Scrub-birds, *Atrichornis*, and Lyrebirds, *Menura* (Passeriformes: Atrichornithidae and Menuridae)

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Abstract. Within *Atrichornis* the two species *A. clamosus* and *A. rufescens* are very similar overall, differing only in characters related to flightlessness, with *A. clamosus* appearing more volant than *A. rufescens*. Similarly, the two species within *Menura* are very similar overall, although *M. novaehollandiae* may be a stronger flyer than *M. alberti*. There are many differences between the genera *Atrichornis* and *Menura*, but the distribution of these character states across the order Passeriformes remains unstudied. What has been noted is that a suite of characters shared by *Menura* and *Atrichornis*, hitherto used to relate the Menurae to the Rhinocryptidae, are also shared by several other genera of birds from a variety of families. We suggest that these characters indicate convergence towards a terrestrial lifestyle and should not be used to indicate phylogenetic proximity.

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Keywords: *Atrichornis,* cursorial adaption, flightlessness, *Menura*, osteology, phylogeny, Rhinocryptidae, volancy.

Until comparatively recently, the relationships of the Australian scrub-birds (*Atrichornis*) and lyrebirds (*Menura*) seemed clear: both genera were closely allied and appeared to form a primitive group, sometimes given subordinal status (Menurae) within the order Passeriformes (Wetmore, 1960; Mayr & Amadon, 1951; Schodde, 1975, amongst others). Sibley (1974) reviewed the taxonomic history of this group and broke with tradition in suggesting that the lyrebirds and scrub-birds should be closely allied to the bowerbird/bird-of-paradise assemblage based on his studies of egg-white proteins. More recent work by Feduccia & Olson (1982) has challenged this view, by pointing out a significant number of osteological differences between the ptilonorhynchids and *Menura*. Work by Raikow (1985) on the appendicular myology of the Menurae and Ptilonorhynchidae/Paradisaeidae assemblage illustrates a number of other differences. Even though Sibley and Ahlquist's most recent work (in press), utilizing DNA × DNA hybridization technique, again closely allies the Menurae and the Ptilonorhynchidae (but no longer the Paradisaeidae), the diversity of opinions clearly indicates that a clear understanding of *Menura* and *Atrichornis* relationships to other songbirds is in the future.

What is also clear from a survey of past and current literature on *Menura* and *Atrichornis* is that their close affinity, although claimed by many authors, is not as well documented as one might believe. Both *Atrichornis* and *Menura* have a relatively simple syrinx that lacks the complexity of muscles present in the oscines. Ames (1971) has suggested this condition is primitive within the Passeriformes. Both *Menura* and *Atrichornis* have, however, an oscine stapes with a flat footplate and a straight bony shaft, a condition also thought to be primitive within the Passeriformes (Feduccia, 1975a, b; Feduccia & Olson, 1982).

Feduccia & Olson (1982) further point out that, besides *Menura* and *Atrichornis*, only members of two other groups, the New Zealand 'wrens' (Acanthisittidae) and some tapaculos (Rhinocryptidae), lack the derived suboscine stapes and the derived oscine syrinx. Their comparisons of members of all these groups led them to conclude that the Menurae (including both *Atrichornis* and *Menura*) were more similar to the Rhinocryptidae than to any other passerine group that they examined, and that both retained a large number

of primitive passeriform characteristics. From this, they suggested a close relationship between these two groups and assumed a close relationship of *Menura* and *Atrichornis* based on a variety of osteological, myological and syringeal characteristics.

In considering those characters that ally *Menura* and *Atrichornis*, and they in turn to the Rhinocryptidae, one of us (RFB) noted a high degree of correlation between such characters and a ground-dwelling, terrestrial mode of life. Examination of birds in the order Passeriformes made it clear that a number of terrestrially adapted species (e.g. *Dasyornis, Orthonyx, Amytornis*, amongst others) also possessed many of those characters that Feduccia and Olson had used to ally the Menurae with the Rhinocryptidae. Thus, we now wonder how many of the shared characters used to ally *Menura* and *Atrichornis* and the Rhinocryptidae are due to convergence towards a common terrestrial lifestyle; and how many are, in fact, due to derivation from a common ancestor. Such a statement applies to all the above taxa, not just the Menurae. Both possibilities need, at this point, to be entertained and tested through well documented studies on a variety of characters across the Passeriformes as a whole, many of which are underway. Until such studies are completed, however, the relationship of such forms as *Menura* and *Atrichornis* will probably remain uncertain.

The purpose of the following study is to document and extensively illustrate the osteology of all the species of *Menura* and *Atrichornis*, which we hope will serve to point out a number of differences that exist between these forms. We also hope that in providing extensive information on these rare forms it will enable workers on passeriform taxonomy and phylogeny access to previously unavailable data that can be used in broad-based comparative studies of this avian order. We further point out that those characters used by Feduccia & Olson (1982) to ally the Menurae and the Rhinocryptidae might have been produced by a similar mode of life and not necessarily by close relationship. We hope such a study will stimulate and encourage further detailed comparative studies of the Passeriformes.

Abbreviations

AMS: Australian Museum, Sydney
ANWC: Australian National Wildlife Collections, CSIRO Division of Wildlife and Rangelands Research, Lyneham
DM: National Museum of New Zealand, Wellington
NMV: Museum of Victoria, Melbourne

Methods and Materials

Traditional classifications which recognized the Menurae utilized plumage, syringeal and osteological characters to delimit this primitive passeriform group. Among the osteological characters were (Sibley, 1974): 1) presence of a curved posterior margin of the sternum, 2) lack of hypocleideum in *Menura*, and 3) presence of only a rudimentary clavicle in *Atrichornis*.

With so few characters forming the osteological evidence, it is obvious that a thorough review of the skeletal system is warranted. In the following study, comparisons of the skeletons of *Atrichornis rufescens, A. clamosus, Menura novaehollandiae* and *M. alberti* are made, as are comparisons of the genera *Menura* and *Atrichornis*.

Comparative material available included: *Atrichornis clamosus*, a skeleton (NMV R11354 ?♀); *A. rufescens*, two partial skeletons (NMV B12407 ♀ + NMV B55794 ♂); *Menura alberti*, two skeletons (AMS 5593 + NMV W10916); and *M. novaehollandiae*, ten skeletons (NMV W Nos. 9655, 8713 and B Nos. 8857, 10398 ♂, 10728, 10729, 10730 ♀, 10731 ♂, 11391, 12391 ♂).

Skeletons were disarticulated and compared on the basis of limb and girdle elements, but comparisons did not include vertebrae, ribs or phalanges. Comparisons between the two species in each genus were made after those of the two genera, using *Menura novaehollandiae* and *Atrichornis clamosus*, the best represented in our sample, as morphotypes.

Osteological Comparison of *Menura* and *Atrichornis*
Fig. 1, Table 1, Plates I–XIX

Comments that follow are based on *Atrichornis clamosus* and *Menura novaehollandiae*.

Cranium. Proportionally, *Menura* is broader and shorter. *Atrichornis* lacks an interorbital septum, *Menura* has partial interorbital septum. Viewed laterally the tympanic wing of the exoccipital extends futher anteriorly in *Atrichornis* but does not extend as far posteriorly as in *Menura*, viewed laterally. Thus, the auditory meatus, in lateral view, is proportionally larger in *Menura*, and not partially closed by bone posteriorly as in *Atrichornis*. The internal mandibular articulation surface of the quadrate is elongate in *Menura* and rounded in *Atrichornis*. The opisthotic of *Menura* is not as inflated as in *Atrichornis*. The foramen magnum of *Menura* is broad and dorsoventrally compressed, whereas in *Atrichornis* it is deeper and mediolaterally compressed. *Menura* has two small openings into the brain case through the posterior wall of the orbit; *Atrichornis* has a single, large fonticulus above a smaller opening.

Rostrum. *Menura* lacks the ossified crest on the culmen that *Atrichornis* displays. The external nares are proportionally more elongated in *Menura*.

Mandible. The medial mandibular process extends further internally and slightly ventral in *Menura*. In *Atrichornis* this process is relatively shorter and curves slightly anteriorly.

Sternum. Note: Only half of the *Atrichornis* sternum (right half) is preserved in NMV R11354 (*A. clamosus*), and thus more information on this element is desired. Shapes of the sterna of *Atrichornis* and *Menura* differ radically, with that of *Atrichornis* being

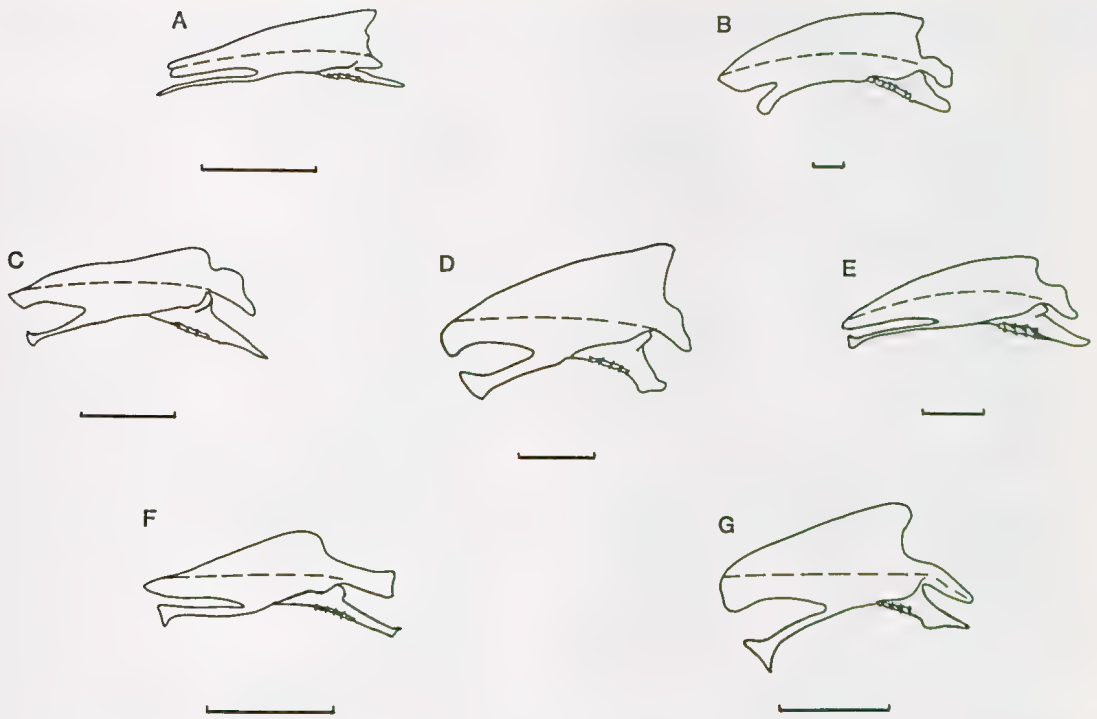

Fig. 1. Lateral views of sterna demonstrating the decreased depth of the sternal keel in non volant birds vs. volant birds: **A** = *Atrichornis clamosus* (NMV R11354); **B** = *Menura novaehollandiae* (NMV W8713); **C** = *Dasyornis broadbenti* (NMV B6839); **D** = *Philemon argenticeps* (ANWC BS101); **E** = *Callaeus cinerea wilsoni* (DM 8637); **F** = *Amytornis woodwardi* (ANWC BS2419); **G** = *Malurus cyaneus* (NMV B10515). Scales = 10 mm.

decidedly more reduced than that of *Menura*. Further differences, some of which are probably related to this whole reduction of the forelimb in *Atrichornis* are as follows. The ventral manubrial spine in *Atrichornis* and *Menura* (viewed ventrally or dorsally) is a narrow spike that bifurcates only slightly at its anterior-most point; in *Menura* this spine broadens into two wings that protrude dorsolaterally at the anterior end of the projection, and the lateral sides of this spine are highly concave, rather than only slightly concave, as they are in *Atrichornis*. The sternum of *Atrichornis*, especially when the posterior lateral processes are excluded, narrows posteriorly, whereas in *Menura* it is about the same width at both its anterior and posterior ends. In *Atrichornis*, the sternocoracoidal processes project far anterior to the ventral manubrial spine and are slender, V-shaped processes; in *Menura* these processes are U-shaped, blunted, and do not project as far forward as the ventral manubrial spine.

In *Atrichornis*, attachments for the costal margins extend half way out onto the sternocoracoidal processes, to the level of the anterior-most projection of the ventral manubrial spine; in *Menura*, the costal margin extends only to the base of the sternocoracoidal process. *Atrichornis* has six costal ribs including, at least in *A. clamosus*, the sixth, which is slender and elongated, appearing to course backwards on the dorsal surface of the sternum, looping down through the deep sternal notch and then curving upward on the outside of the posterior lateral process (more specimens are needed to confirm this, as it may be an artifact of preparation); *Menura* has five well defined intercostal spaces that indicate at least five costal ribs are present, but the sternal notch is so small and so far posterior to the last intercostal space, that it is doubtful whether a sixth costal rib would loop through that notch as it does in *Atrichornis*. *Atrichornis* has a single, deep sternal notch on either side of the sternum and an elongate, slender posterior lateral process that is convex laterally and somewhat flattened and rounded at its posterior tip; the notch is about half the length of the sternum. In *Menura* the notch is an insignificant incision in the outer part of the posterior margin of the sternum, and the resultant posterior process is short and broad. Dorsally, the sternum of *Atrichornis* is distinctly less concave than that of *Menura*, especially near the anterior end where pronounced basins are formed in *Menura*, one at the base of either sternocoracoidal process and a third median one at the anterior end just posterior to the medial margin of the coracoidal sulcus. Ventrally, the coracoidal sulci in *Atrichornis* are oriented to form an angle of about 75–80° with the carina, whereas in *Menura* they form an angle of about 40° with the carina. In lateral view, the carina in *Atrichornis* extends as far forward as, perhaps slightly farther than, the ventral manubrial spine; in *Menura* the ventral manubrial spine extends decidely beyond the carina. In overall proportions, the sternum of *Menura* is more than twice as long as it is wide; in *Atrichornis* it is only slightly longer than it is wide.

Table 1. Measurements (in mm) of osteological material of *Atrichornis* and *Menura*: A, *Atrichornis clamosus*; B, *A. rufescens*; C, *Menura novaehollandiae*: D, *M. alberti*. > greater than; ~ approximately.

CRANIUM

WIDTH AT THE THE ORBITS

	A	B	C	D
Mean	4.2	0	18.9	20.1
Maximum value	4.2	0	21.6	20.1
Minimum value	4.2	0	16.2	20.0
Variance	0	0	3.3	0
Standard deviation	0	0	1.8	0.1
Total number	1	0	9	2

GREATEST WIDTH

	A	B	C	D
Mean	22.2	0	34.8	34.2
Maximum value	22.2	0	36.7	35.3
Minimum value	22.2	0	32.0	33.0
Variance	0	0	3.0	2.6
Standard deviation	0	0	1.7	1.6
Total number	1	0	8	2

GREATEST LENGTH

	A	B	C	D
Mean	17.2	0	49.4	48.5
Maximum value	17.2	0	52.0	48.8
Minimum value	17.2	0	47.0	48.2
Variance	0	0	2.8	0.2
Standard deviation	0	0	1.7	0.4
Total number	1	0	9	2

ROSTRUM

TOTAL LENGTH

	A	B	C	D
Mean	0	0	38.7	40.2
Maximum value	0	0	42.5	40.9
Minimum value	0	0	36.7	39.4
Variance	0	0	3.6	1.1
Standard deviation	0	0	1.9	1.1
Total number	0	0	8	2

LENGTH OF EXTERNAL NARES

	A	B	C	D
Mean	0	0	19.8	21.0
Maximum value	0	0	21.3	21.3
Minimum value	0	0	18.9	20.6
Variance	0	0	0.7	0.2
Standard deviation	0	0	0.8	0.5
Total number	0	0	9	2

MANDIBLE

GREATEST LENGTH

	A	B	C	D
Mean	0	0	69.1	69.6
Maximum value	0	0	71.5	69.7
Minimum value	0	0	65.5	69.5
Variance	0	0	4.6	0
Standard deviation	0	0	2.2	0.1
Total number	0	0	8	2

GREATEST DEPTH

	A	B	C	D
Mean	2.4	0	4.4	5.2
Maximum value	2.4	0	4.8	5.2
Minimum value	2.4	0	3.8	5.1
Variance	0	0	0.1	0
Standard deviation	0	0	0.3	0.1
Total number	1	0	9	2

WIDTH ACROSS PROC. MAND. MEDIALIS

	A	B	C	D
Mean	3.6	0	10.3	11.2
Maximum value	3.6	0	10.8	11.5
Minimum value	3.6	0	10.1	10.9
Variance	0	0	0.1	0.2
Standard deviation	0	0	0.3	0.4
Total number	1	0	9	2

STERNUM

MAXIMUM LENGTH ALONG MIDLINE

	A	B	C	D
Mean	>17.8	>12.3	80.4	72.5
Maximum value	>17.8	>12.3	86.8	72.5
Minimum value	>17.8	>12.3	70.2	72.5
Variance	0	0	41.6	0
Standard deviation	0	0	6.4	0
Total number	1	1	7	1

WIDTH ACROSS STERNOCORACOIDIAL PROC.

	A	B	C	D
Mean	~11.6	9.6	31.6	30.3
Maximum value	~11.6	9.6	34.6	30.3
Minimum value	~11.6	9.6	28.4	30.3
Variance	0	0	4.9	0
Standard deviation	0	0	2.2	0
Total number	1	1	8	1

DISTANCE BETWEEN ANTERIOR END OF STERNOCORACOIDAL PROC. AND POSTERIOR END OF COSTAL AREA

	A	B	C	D
Mean	11	7.9	28.2	29.5
Maximum value	11	7.9	30.5	29.5
Minimum value	11	7.9	24.1	29.5
Variance	0	0	4.3	0
Standard deviation	0	0	2.1	0
Total number	1	1	8	1

DISTANCE FROM DORSAL TIP OF VENTRAL MANUBRIAL SPINE TO CARINAL APEX

	A	B	C	D
Mean	5.3	3.4	21.9	23.6
Maximum value	5.3	~3.4	23.4	25.2
Minimum value	5.3	~3.4	20.3	22.0
Variance	0	0	1	5.1
Standard deviation	0	0	1	2.3
Total number	1	1	7	2

PELVIS

MAXIMUM LENGTH (NOT INCLUDING PUBIS)

	A	B	C	D
Mean	23.3	18.3	73.1	72.9
Maximum value	23.3	18.3	78.7	76.3
Minimum value	23.3	18.3	69.2	69.4
Variance	0	0	14.1	23.8
Standard deviation	0	0	3.7	4.9
Total number	1	1	6	2

MAXIMUM WIDTH ACROSS ANTITROCHANTER

	A	B	C	D
Mean	13.9	12.2	45.2	41.8
Maximum value	13.9	12.2	49.3	41.8
Minimum value	13.9	12.2	42.2	41.8
Variance	0	0	8.2	0
Standard deviation	0	0	2.9	0
Total number	1	1	5	1

MAXIMUM WIDTH OF ANTERIOR END

	A	B	C	D
Mean	7.2	6.2	31.3	27.5
Maximum value	7.2	6.2	34.6	31.7
Minimum value	7.2	6.2	29.0	23.2
Variance	0	0	3.3	36.1
Standard deviation	0	0	1.8	6.0
Total number	1	1	6	2

MAXIMUM WIDTH OF POSTERIOR END MEASURED ON DORSAL SURFACE

	A	B	C	D
Mean	8.6	7.8	44.3	42.2
Maximum value	8.6	7.8	48.7	42.2
Minimum value	8.6	7.8	40.0	42.2
Variance	0	0	10.9	0
Standard deviation	0	0	3.3	0
Total number	1	1	6	1

LENGTH FROM POSTERIOR END OF ANTITROCHANTER TO ANTERIOR END OF ELEMENT

	A	B	C	D
Mean	15.1	12.9	45.1	44.6
Maximum value	15.1	12.9	49.8	46.0
Minimum value	15.1	12.9	42.5	43.2
Variance	0	0	7.8	3.9
Standard deviation	0	0	2.8	2.0
Total number	1	1	6	1

LENGTH OF SYNSACRUM FROM POSTERIOR END OF ANTITROCHANTER TO POSTERIOR END OF ELEMENT

	A	B	C	D
Mean	9.9	7.4	29.9	31.7
Maximum value	9.9	7.4	32.1	33.5
Minimum value	9.9	7.4	28.2	29.8
Variance	0	0	2.2	6.8
Standard deviation	0	0	1.5	2.6
Total number	1	1	7	2

DEPTH OF PELVIS AT POSTERIOR END FROM DORSALMOST PART OF ILIUM TO BASE OF ISCHIUM

	A	B	C	D
Mean	10.5	8.8	32.4	29.7
Maximum value	10.5	~8.8	36.0	31.4
Minimum value	10.5	~8.8	28.6	27.9
Variance	0	0	7.8	6.1
Standard deviation	0	0	2.8	2.5
Total number	1	1	5	2

SCAPULA

MAXIMUM MEASUREMENT ACROSS ACROMION TO DISTAL PART OF GLENOID FACET

	A	B	C	D
Mean	4.2	3.0	11.7	11.3
Maximum value	4.2	3.0	13.4	11.3
Minimum value	4.2	3.0	9.9	11.3
Variance	0	0	1.0	0
Standard deviation	0	0	1.0	0
Total number	1	1	9	1

MAXIMUM DEPTH ACROSS ACROMION

	A	B	C	D
Mean	2.6	1.3	6.5	6.5
Maximum value	2.6	1.3	7.2	6.5
Minimum value	2.6	1.3	5.9	6.5
Variance	0	0	0.2	0
Standard deviation	0	0	0.5	0
Total number	1	1	8	1

MAXIMUM LENGTH

	A	B	C	D
Mean	21.6	16.5	59.9	59.5
Maximum value	21.6	16.5	63.3	61.5
Minimum value	21.6	16.5	54.6	57.5
Variance	0	0	8.9	8.0
Standard deviation	0	0	3	2.8
Total number	1	1	9	2

WIDTH OF SHAFT AT DISTAL END OF GLENOID FACET

	A	B	C	D
Mean	1.6	2.0	5.7	5.5
Maximum value	1.6	2.0	6.6	5.8
Minimum value	1.6	2.0	4.5	5.2
Variance	0	0	0.5	0.2
Standard deviation	0	0	0.7	0.4
Total number	1	1	7	2

CORACOID

TOTAL LENGTH FROM DORSALMOST END TO TIP OF STERNOCORACOIDAL PROCESS

	A	B	C	D
Mean	19.6	15.2	42.8	42.9
Maximum value	19.6	15.2	44.7	43.9
Minimum value	19.6	15.2	38.8	41.8
Variance	0	0	3.5	2.2
Standard deviation	0	0	1.9	1.5
Total number	1	1	8	2

DORSAL WIDTH FROM BRACHIAL TUBEROSITY EXTENSION ACROSS GLENOID FACET

	A	B	C	D
Mean	2.6	1.2	8.9	9.1
Maximum value	2.6	~1.2	9.6	9.2
Minimum value	2.6	~1.2	7.7	9.0
Variance	0	0	0.4	0
Standard deviation	0	0	0.6	0.1
Total number	1	1	8	2

MAXIMUM WIDTH OF VENTRAL END

	A	B	C	D
Mean	3.2	2.5	12.5	11.6
Maximum value	3.2	2.5	15.0	12.6
Minimum value	3.2	2.5	10.2	10.5
Variance	0	0	3.0	2.2
Standard deviation	0	0	1.7	1.5
Total number	1	1	8	2

LENGTH FROM DORSALMOST EXTENSION OF CORACOHUMERAL SURFACE TO VENTRAL PART OF SCAPULAR FACET

	A	B	C	D
Mean	3.8	2.6	12.1	11.4
Maximum value	3.8	2.6	12.7	12.0
Minimum value	3.8	2.6	11.4	10.8
Variance	0	0	0.2	0.7
Standard deviation	0	0	0.4	0.8
Total number	1	1	7	2

CLAVICLES

MAXIMUM LENGTH FROM SCAPULAR TUBEROSITY TO SYMPHYSIS

	A	B	C	D
Mean	7.6	0	40.2	36.6
Maximum value	>7.6	0	44.3	36.6
Minimum value	>7.6	0	37.9	36.6
Variance	0	0	6.2	0
Standard deviation	0	0	2.5	0
Total number	1	0	8	1

MAXIMUM WIDTH ACROSS SCAPULAR TUBEROSITY AND CORACOIDAL FACET

	A	B	C	D
Mean	2.6	0	8.1	7.1
Maximum value	2.6	0	9.4	7.1
Minimum value	2.6	0	7.0	7.1
Variance	0	0	0.7	0
Standard deviation	0	0	0.8	0
Total number	1	0	8	1

HUMERUS

TOTAL LENGTH

	A	B	C	D
Mean	5.0	3.4	63.3	61.7
Maximum value	5.0	3.4	66.5	61.7
Minimum value	5.0	3.4	59.5	61.7
Variance	0	0	6.1	0
Standard deviation	0	0	2.5	0
Total number	1	1	7	1

MAXIMUM WIDTH ACROSS PROXIMAL END

	A	B	C	D
Mean	5.0	3.4	17.7	16.9
Maximum value	5.0	3.4	19.9	17.6
Minimum value	5.0	3.4	15.1	16.1
Variance	0	0	1.9	1.1
Standard deviation	0	0	1.4	1.1
Total number	1	1	9	2

DEPTH OF INTERNAL TUBEROSITY

	A	B	C	D
Mean	2.1	2.2	6.1	5.7
Maximum value	2.1	2.2	6.7	5.9
Minimum value	2.1	2.2	5.5	5.5
Variance	0	0	0.2	0.1
Standard deviation	0	0	0.4	0.3
Total number	1	1	9	2

MAXIMUM DEPTH OF HEAD

	A	B	C	D
Mean	1.4	1.1	5.3	5.2
Maximum value	1.4	1.1	5.9	5.3
Minimum value	1.4	1.1	4.8	5.0
Variance	0	0	0.1	0
Standard deviation	0	0	0.4	0.2
Total number	1	1	9	2

MAXIMUM WIDTH OF DISTAL END

	A	B	C	D
Mean	4.5	0	15.4	15.5
Maximum value	4.5	0	16.8	15.5
Minimum value	4.5	0	14.0	15.5
Variance	0	0	0.8	0
Standard deviation	0	0	0.9	0
Total number	1	0	9	1

MAXIMUM DEPTH OF EXTERNAL CONDYLE

	A	B	C	D
Mean	2.1	0	6.8	7
Maximum value	2.1	0	7.9	7.2
Minimum value	2.1	0	5.9	6.7
Variance	0	0	0.4	0.1
Standard deviation	0	0	0.7	0.4
Total number	1	0	9	2

MAXIMUM DEPTH OF INTERNAL CONDYLE

	A	B	C	D
Mean	1.1	0	3.8	4.1
Maximum value	1.1	0	4.4	4.3
Minimum value	1.1	0	3.0	3.9
Variance	0	0	0.3	0.1
Standard deviation	0	0	0.5	0.3
Total number	1	0	9	2

LENGTH OF INTERNAL CONDYLE

	A	B	C	D
Mean	1.2	0	5.4	4.0
Maximum value	1.2	0	6.6	4.0
Minimum value	1.2	0	4.0	4.0
Variance	0	0	1.0	0
Standard deviation	0	0	1.0	0
Total number	1	0	8	1

LENGTH OF EXTERNAL CONDYLE

	A	B	C	D
Mean	1.4	0	5.0	5.2
Maximum value	1.4	0	6.2	5.2
Minimum value	1.4	0	4.0	5.2
Variance	0	0	0.6	0
Standard deviation	0	0	0.7	0
Total number	1	0	8	1

RADIUS

TOTAL LENGTH

	A	B	C	D
Mean	14.8	0	58.8	56.8
Maximum value	~14.8	0	62.5	57.8
Minimum value	~14.8	0	55.2	55.8
Variance	0	0	5.3	2.0
Standard deviation	0	0	2.3	1.4
Total number	1	0	9	2

MAXIMUM MEASUREMENT ACROSS PROXIMAL END

	A	B	C	D
Mean	1.3	0	4.9	5.1
Maximum value	1.3	0	5.6	5.4
Minimum value	1.3	0	3.6	4.7
Variance	0	0	0.4	0.2
Standard deviation	0	0	0.6	0.5
Total number	1	0	9	2

MAXIMUM MEASUREMENT ACROSS DISTAL END

	A	B	C	D
Mean	1.6	0	6.2	6.2
Maximum value	1.6	0	7.0	6.6
Minimum value	1.6	0	5.5	5.8
Variance	0	0	0.2	0.3
Standard deviation	0	0	0.5	0.6
Total number	1	0	9	2

MEASUREMENT OF DISTAL END ACROSS LIGAMENTAL PROMINENCE

	A	B	C	D
Mean	0.9	0	3.4	3.1
Maximum value	0.9	0	3.7	3.4
Minimum value	0.9	0	3.0	2.7
Variance	0	0	0.1	0.2
Standard deviation	0	0	0.2	0.5
Total number	1	0	8	2

ULNA

MAXIMUM LENGTH

	A	B	C	D
Mean	16.4	0	65.8	63.7
Maximum value	16.4	0	69.9	65.1
Minimum value	16.4	0	60.1	62.3
Variance	0	0	9.9	3.9
Standard deviation	0	0	3.1	2.0
Total number	1	0	9	2

MAXIMUM WIDTH OF PROXIMAL END

	A	B	C	D
Mean	2.8	0	10.3	9.7
Maximum value	2.8	0	11.2	10.5
Minimum value	2.8	0	9.4	8.9
Variance	0	0	0.3	1.3
Standard deviation	0	0	0.5	1.1
Total number	1	0	9	2

MAXIMUM WIDTH OF DISTAL END

	A	B	C	D
Mean	2.6	0	8.3	8.8
Maximum value	2.6	0	9.0	9.3
Minimum value	2.6	0	8.0	8.3
Variance	0	0	0.1	0.5
Standard deviation	0	0	0.3	0.7
Total number	1	0	9	2

DEPTH OF EXTERNAL CONDYLE

	A	B	C	D
Mean	2.1	0	7.7	7.3
Maximum value	2.1	0	8.5	7.6
Minimum value	2.1	0	6.8	6.9
Variance	0	0	0.3	0.2
Standard deviation	0	0	0.5	0.5
Total number	1	0	9	2

LENGTH OF INTERNAL COTYLA

	A	B	C	D
Mean	1.9	0	6.3	5.9
Maximum value	1.9	0	7.0	6.0
Minimum value	1.9	0	5.5	5.7
Variance	0	0	0.2	0
Standard deviation	0	0	0.5	0.2
Total number	1	0	9	2

LENGTH FROM DISTAL END OF INTERNAL COTYLA TO PROXIMAL END OF OLECRANON

	A	B	C	D
Mean	2.9	0	9.8	9.5
Maximum value	2.9	0	10.5	9.7
Minimum value	2.9	0	8.5	9.3
Variance	0	0	0.4	0.1
Standard deviation	0	0	0.6	0.3
Total number	1	0	9	2

CARPOMETACARPUS

MAXIMUM LENGTH

	A	B	C	D
Mean	10	0	38.3	36.3
Maximum value	10	0	41.3	38.1
Minimum value	10	0	35.3	34.5
Variance	0	0	3.9	6.5
Standard deviation	0	0	2.0	2.5
Total number	1	0	9	2

MAXIMUM WIDTH ACROSS TROCHLEAE

	A	B	C	D
Mean	1.7	0	5.4	5.1
Maximum value	1.7	0	5.7	5.4
Minimum value	1.7	0	5.0	4.8
Variance	0	0	0.1	0.2
Standard deviation	0	0	0.3	0.4
Total number	1	0	9	2

MAXIMUM DEPTH (TROCHLEAE TO METACARPAL I)

	A	B	C	D
Mean	3.5	0	12.2	11.4
Maximum value	3.5	0	13.3	11.6
Minimum value	3.5	0	11.2	11.1
Variance	0	0	0.4	0.1
Standard deviation	0	0	0.6	0.4
Total number	1	0	9	2

LENGTH OF INTERMETACARPAL SPACE

	A	B	C	D
Mean	2.9	0	14.8	14.1
Maximum value	2.9	0	17.2	14.5
Minimum value	2.9	0	14.3	13.6
Variance	0	0	0.8	0.4
Standard deviation	0	0	0.9	0.6
Total number	1	0	9	2

DEPTH ACROSS FACETS FOR DIGITS II AND III

	A	B	C	D
Mean	2.2	0	8.1	7.9
Maximum value	2.2	0	8.9	8.0
Minimum value	2.2	0	7.3	7.8
Variance	0	0	0.2	0
Standard deviation	0	0	0.5	0.1
Total number	1	0	9	2

FEMUR

TOTAL LENGTH

	A	B	C	D
Mean	27.1	20.4	71.2	68.3
Maximum value	27.1	>20.4	75.9	69.2
Minimum value	27.1	>20.4	67.8	67.3
Variance	0	0	8.4	1.8
Standard deviation	0	0	2.9	1.3
Total number	1	1	9	2

MAXIMUM WIDTH OF PROXIMAL END

	A	B	C	D
Mean	4.7	4.3	18.4	17.2
Maximum value	4.7	4.3	20.8	17.7
Minimum value	4.7	4.3	16.0	16.7
Variance	0	0	1.8	0.5
Standard deviation	0	0	1.3	0.7
Total number	1	1	9	2

DEPTH OF HEAD

	A	B	C	D
Mean	1.8	1.4	8.4	8.3
Maximum value	1.8	1.4	9.1	8.7
Minimum value	1.8	1.4	7.7	7.9
Variance	0	0	0.2	0.3
Standard deviation	0	0	0.5	0.6
Total number	1	1	9	2

DEPTH OF TROCHANTER

	A	B	C	D
Mean	3.6	2.6	12.1	11.5
Maximum value	3.6	2.6	14.2	11.9
Minimum value	3.6	2.6	10.9	11.0
Variance	0	0	1.0	0.4
Standard deviation	0	0	1.0	0.6
Total number	1	1	9	2

MAXIMUM LENGTH OF TROCHANTERIC RIDGE

	A	B	C	D
Mean	5.5	3.0	22.3	21.8
Maximum value	5.5	3.0	25.8	22.1
Minimum value	5.5	3.0	20.4	21.4
Variance	0	0	4.3	0.2
Standard deviation	0	0	2.1	0.5
Total number	1	1	9	2

MAXIMUM WIDTH OF DISTAL END

	A	B	C	D
Mean	4.6	0	18.4	17.6
Maximum value	4.6	0	20.0	18.4
Minimum value	4.6	0	16.4	16.8
Variance	0	0	1.2	1.3
Standard deviation	0	0	1.1	1.1
Total number	1	0	9	2

MAXIMUM DEPTH OF INTERNAL CONDYLE

	A	B	C	D
Mean	3.7	0	9.9	9.4
Maximum value	3.7	0	11.0	10.1
Minimum value	3.7	0	8.7	8.6
Variance	0	0	0.5	1.1
Standard deviation	0	0	0.7	1.1
Total number	1	0	9	2

MAXIMUM DEPTH OF EXTERNAL CONDYLE

	A	B	C	D
Mean	3.7	0	13.5	13.1
Maximum value	3.7	0	14.8	13.4
Minimum value	3.7	0	11.9	12.8
Variance	0	0	0.7	0.2
Standard deviation	0	0	0.8	0.4
Total number	1	0	9	2

TIBIOTARSUS

TOTAL LENGTH

	A	B	C	D
Mean	40.2	35.6	136.2	137.4
Maximum value	40.2	35.6	144.0	143.4
Minimum value	40.2	35.6	127.2	131.3
Variance	0	0	26.4	73.2
Standard deviation	0	0	5.1	8.6
Total number	1	1	8	2

LENGTH OF FIBULAR CREST

	A	B	C	D
Mean	6.3	4.4	20.0	22.2
Maximum value	6.3	~4.4	23.5	23.1
Minimum value	6.3	~4.4	16.3	21.2
Variance	0	0	4.5	1.8
Standard deviation	0	0	2.1	1.3
Total number	1	1	9	2

ANTERIOR WIDTH OF PROXIMAL END

	A	B	C	D
Mean	5.4	0	23.1	23.0
Maximum value	5.4	0	24.6	24.4
Minimum value	5.4	0	21.1	21.5
Variance	0	0	1.4	4.2
Standard deviation	0	0	1.2	2.1
Total number	1	0	9	2

POSTERIOR WIDTH OF PROXIMAL END

	A	B	C	D
Mean	4.5	0	15.6	15.1
Maximum value	4.5	0	17.0	15.9
Minimum value	4.5	0	13.6	14.2
Variance	0	0	0.8	1.4
Standard deviation	0	0	0.9	1.2
Total number	1	0	9	2

MAXIMUM WIDTH OF DISTAL END

	A	B	C	D
Mean	3.7	3.0	13.9	14.2
Maximum value	3.7	3.0	14.9	15.5
Minimum value	3.7	3.0	12.5	12.8
Variance	0	0	0.6	3.6
Standard deviation	0	0	0.8	1.9
Total number	1	1	9	2

DEPTH OF INTERNAL CONDYLE

	A	B	C	D
Mean	3.5	2.9	12.2	12.1
Maximum value	3.5	2.9	13.3	12.9
Minimum value	3.5	2.9	10.8	11.2
Variance	0	0	0.5	1.4
Standard deviation	0	0	0.7	1.2
Total number	1	1	9	2

DEPTH OF EXTERNAL CONDYLE

	A	B	C	D
Mean	0	2.6	11.5	11.4
Maximum value	0	2.6	12.9	12.3
Minimum value	0	2.6	10.3	10.5
Variance	0	0	0.6	1.6
Standard deviation	0	0	0.8	1.3
Total number	0	1	9	2

TARSOMETATARSUS

TOTAL LENGTH

	A	B	C	D
Mean	26.1	22.1	112.3	108.8
Maximum value	26.1	22.1	121.2	112.6
Minimum value	26.1	22.1	100.7	104.9
Variance	0	0	53.0	29.6
Standard deviation	0	0	7.3	5.4
Total number	1	1	9	2

WIDTH OF PROXIMAL END

	A	B	C	D
Mean	4.0	3.3	14.9	12.7
Maximum value	4.0	3.3	15.9	13.8
Minimum value	4.0	3.3	13.5	11.5
Variance	0	0	0.8	2.6
Standard deviation	0	0	0.9	1.6
Total number	1	1	9	2

DEPTH OF PROXIMAL END

	A	B	C	D
Mean	3.5	0	13.7	13.8
Maximum value	3.5	0	14.5	14.2
Minimum value	3.5	0	11.9	13.3
Variance	0	0	0.7	0.4
Standard deviation	0	0	0.8	0.6
Total number	1	0	9	2

WIDTH OF DISTAL END

	A	B	C	D
Mean	3.6	3.3	13.3	14.6
Maximum value	3.6	3.3	14.5	14.6
Minimum value	3.6	3.3	11.9	14.6
Variance	0	0	0.6	0
Standard deviation	0	0	0.8	0
Total number	1	1	9	1

MAXIMUM DEPTH OF DISTAL END

	A	B	C	D
Mean	1.7	1.5	6.3	6.1
Maximum value	1.7	1.5	7.2	6.4
Minimum value	1.7	1.5	5.6	~5.7
Variance	0	0	0.2	0.2
Standard deviation	0	0	0.5	0.5
Total number	1	1	9	2

Synsacrum. In dorsal view, the sacral area between the posterior iliac crests is flattened in *Menura*, but curved in an arch from anterior to posterior in *Atrichornis*. The synsacrum of *Menura*, in dorsal view, has two distinct lateral processes, one on either side, that protrude beyond the contours of the anterior iliac crest; *Atrichornis* lacks these. In dorsal view, the contours of the anterior iliac crest in *Menura* are curved over the entire length, markedly concave laterally; in *Atrichornis*, although slightly concave, the crest is straight over much of its length. In *Menura*, the anterior part of the iliac crest grades into the posterior iliac crest without interruption; a distinct crest exists over the entire length, whereas in *Atrichornis* a distinct break occurs where no definable ridge is present. In dorsal view, the lateral border of the ilium in *Menura* is slightly convex laterally, then slightly concave near the posterior end, smoothly grading into distinct posterior projections. In *Atrichornis* the lateral border is strongly flexed and L-shaped, producing an elongate, slender projection. In dorsal view, in *Menura*, the anterior iliac crest terminates dorsal to, and at the same level as, the antitrochanter; in *Atrichornis* the crest ends distinctly posterior to the antitrochanter. The dorsal border of the synsacrum, in lateral view, is more highly curved in *Atrichornis* than in *Menura* where it is nearly a straight, rather than a curved line, convex dorsally. In lateral view, the angle formed between the anterior part of the ilium and pubis in the area round the acetabulum is a small obtuse one in *Atrichornis* and a large obtuse angle in *Menura*, thus giving *Atrichornis* a much more highly arched appearance. The ischiopublic fenestra, in lateral view, is decidedly larger with respect to overall size of the synsacrum in *Atrichornis* than in *Menura*, thus rendering the posteroventral process of the ischium much more slender than that in *Menura*. In lateral view, the posterior border of ilium and ischium is more deeply incised (concave posteriorly) dorsally in *Menura* than in *Atrichornis*. The posterior process of ilium just dorsal to this area is directed posterodorsally in *Atrichornis*, but posteroventrally in *Menura*. In lateral view, the ischial angle forms a short process extending only a short distance ventral to the obturator foramen in *Menura*; in *Atrichornis* this angle forms an elongate process that extends far ventral to the obturator foramen. In lateral view, the ilioischiatic fenestra is large in *Menura*, but very large in *Atrichornis*. In ventral view, the ventral border of synsacral vertebrae is planar, flat in *Menura*, whereas in *Atrichornis* it is highly concave ventrally near the posterior end; this results in the posterior decurvature of the *Atrichornis* synsacrum. In ventral view, the posterior end of synsacrum is more inflated in *Menura* with the result that two deep fossae are present, one on either side of the midline extending back into the ilium in *Menura*. No such fossae occur in *Atrichornis*.

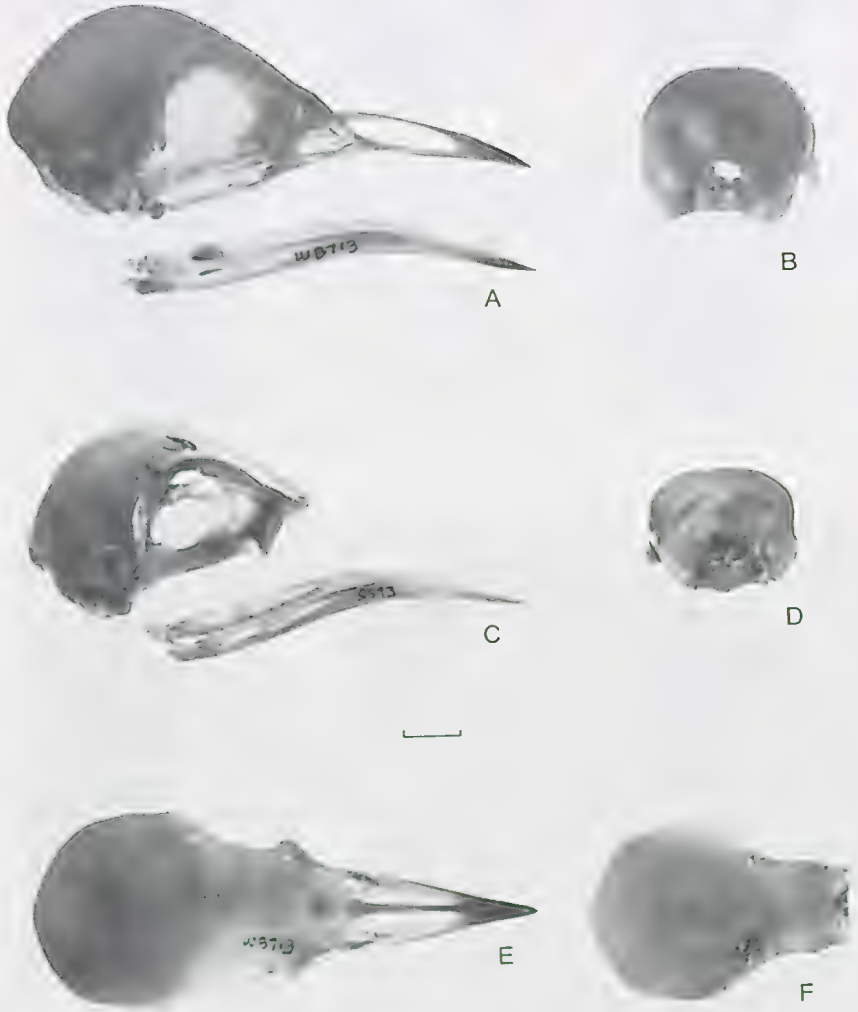

Plate I. Skulls of *Menura*. A, B, E: *M. novaehollandiae* (NMV W8713); C, D, F: *M. alberti* (AM S593). A, C: lateral; B, D: posterior; E, F: dorsal views. Scale = 10 mm.

Plate II. Skulls and shoulder girdle elements of *Menura*. A, C, E, G, I, K: *M. novaehollandiae* (NMV W8713); B, D, F, H, J, L: *M. alberti* (AM S593). A, B: scapulae, dorsal view; C, D: scapulae, distal or articular view; E, F: coracoids, internal view; I, J: coracoids, external view; G, H, K, L: skulls, ventral view. Scales = 10 mm. Single scale applies to G, K; single scale applies to H, I, J, L.

Scapula. In both *Menura* and *Atrichornis* the acromion bifurcates into two blunt, knob-like processes. In *Menura*, these two are nearly equal in size, whereas in *Atrichornis* the dorsal-most is distinctly more elongate and more bulky than the second. Also in *Menura*, both processes extend about an equal distance anteriorly, whereas in *Atrichornis* the ventral process extends farther anteriorly.

Coracoid. The following observations are viewed dorsally (distally). *Menura* has an elongate, blunt process that extends ventrally from the brachial tuberosity, whereas *Atrichornis* lacks any process in this area. In *Menura*, the area beneath the brachial tuberosity is deeply excavated with a pneumatic fossa accompanying this; in *Atrichornis* this area is rather flattened or only slightly curved and has no fossa. In *Menura*, when the distal (dorsal) end of the coracoid is viewed, the coracohumeral surface is twisted only slightly away from a plane defined by the dorsal surface of the coracoidal shaft; in *Atrichornis*, the coracohumeral surface is twisted anteriorly to a much greater degree, forming a large acute angle with the coracoidal shaft plane. In both *Menura* and *Atrichornis*, coracoids are elongate and slender, and the (dorsal) ends, when viewed anteriorly, are rather similar, except that *Atrichornis* lacks a process from the brachial tuberosity; the coracoid of *Atrichornis* is relatively more slender than that of *Menura*.

The following observations are viewed anteriorly (ventrally). *Menura* has a distinct, well-defined ridge for muscle attachment bordering the proximolateral side of coracoidal shaft; in *Atrichornis* the ridge is only slightly indicated. In *Menura*, the coracoid shaft expands more broadly ventrally with development of a reduced sternocoracoidal process, whereas this process flares only slightly in *Atrichornis*, and no distinct sternocoracoidal process is developed. In *Menura* a distinct process courses dorsally from the internal distal angle; *Atrichornis* lacks this process. The lateral end of the sternal face in *Menura* extends further ventrally than the medial part of the facet; in *Atrichornis* both medial and lateral parts of the sternal facet extend about the same distance ventrally. In *Menura*, a distinct notch is present along the internal border of the shaft just dorsal to a point where the shaft begins to flare for the ventral end; no notch is present in *Atrichornis*. As viewed proximally: in *Menura* the coracoid is slightly arched, and concave posteriorly; (dorsally) *Atrichornis* is more highly arched.

Clavicles. The clavicles in *Atrichornis* are extremely reduced (they are somewhat reminiscent of a rib in shape), not even fusing along the midline as they do in *Menura*. In *Atrichornis*, the individual clavicle is nearly T-shaped, with the scapular tuberosity being slightly more elongate than the process extending in the opposite direction bearing the coracoidal facet. In *Menura*, the expansion at the dorsal end of the shaft for the scapular tuberosity and coracoidal facet is more bulbous, and the angle between one line joining the scapular tuberosity and the coracoidal facet, and another line following the shaft of the clavicle, is distinctly less than 90°.

Humerus. In anconal view, the pneumatic fossa is more deeply excavated in *Menura*, the excavation leading far into the interior of the bone. In *Atrichornis*, the fossa is closed off at the bottom of a considerable excavation with no indication of connection with the interior parts of the bone. In *Atrichornis*, the proximal part of the shaft just distal to the pneumatic fossa is deeply excavated, and this excavation leads directly into the pneumatic fossa. This excavation does not occur in *Menura*. The deltoid crest extends relatively further palmad (or, in other words, it is better developed) in *Menura* than in *Atrichornis* where it is generally low and rounded. When viewed proximally, the deltoid crest simply extends further from the shaft in *Menura*. In proximal view, the palmar and anconal margins of the head are straight and parallel at right angles to the internal tuberosity in *Atrichornis*, whereas in *Menura*, the external and internal margins converge and are concave palmarly. *Atrichornis* differs from *Menura* in having a deep excavation along the internal border of the shaft (viewed palmarly) just proximal to the entepicondyle; a distinct, much shallower depression is indicated in this region in *Menura*. In *Atrichornis*, the entepicondyle extends farther distally beyond the internal and external condyles than in *Menura*. In *Atrichornis*, the internal and external condyles are more nearly the same proximodistal length, the external slightly exceeding the internal, whereas the disparity between those of *Menura* is much greater. In *Atrichornis*, the area between the entepicondylar prominence and the more lateral and prominent anterior articular ligament is depressed (concave palmarly), whereas in *Menura* it is not excavated at all, but flat. In ventral view, *Atrichornis* has a slight depression for the *pronator brevis*, not a relatively marked one, as in *Menura*, just anconal to the entepicondylar prominence. In dorsal view, the proximal end of the ectepicondylar prominence is located about twice the length of the external condyle away from the distal end of the humerus in *Atrichornis*, whereas in *Menura* it is situated only slightly proximal to the proximal end of the external condyle. In distal view, the entepicondyle in *Atrichornis* is relatively more inflated than in *Menura*.

Radius. There are very few differences between the radii of *Menura* and *Atrichornis*. The only major difference noted was that, relative to the thickness of the ulna, the radius in *Atrichornis* is much slighter than in *Menura*.

Ulna. The feather papillae are much more prominent in *Menura* than in *Atrichornis*. The shaft of the ulna in *Menura* is slightly curved, concave palmarly, but not as highly curved as in *Atrichornis*. In proximal view, the palmar border of the proximal articular surface is much more deeply incised between the internal and external cotylae in *Menura* than in *Atrichornis*. The olecranon in *Menura* is displaced farther internally than

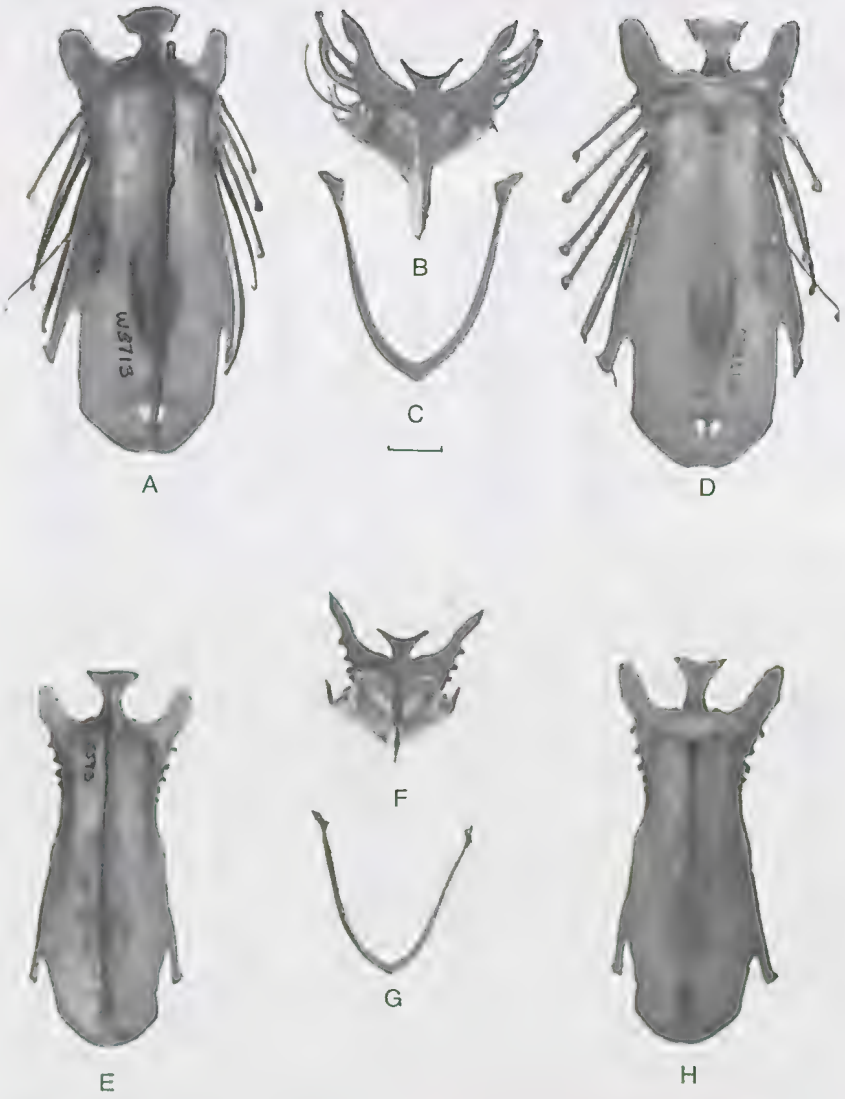

Plate III. Sterna and furcula of *Menura*. A–D: *M. novaehollandiae* (NMV W8713); E–H: *M. alberti* (AM S593). A, E: sterna, ventral view; B, F: sterna, anterior view; D, H: sterna, dorsal view; C, G: furcula, posterior view. Scale = 10 mm.

Plate IV. Synsacra of *Menura*. A–C: *M. novaehollandiae* (NMV W8713); D–F: *M. alberti* (AM S593). A, D: dorsal view; B, E: lateral view; C, F: ventral view. Scale = 10 mm.

it is in *Atrichornis*.

Carpometacarpus. The ligamental attachment of the pisiform process is much more prominent in *Menura* than in *Atrichornis*. In *Menura* the process is a single prominence, whereas in *Atrichornis* two low prominences are present. In *Menura*, the external ligamental attachment is much more prominent than in *Atrichornis*. The carpometacarpus is proportionally stouter in *Atrichornis* than it is in *Menura*. A prominence that is represented only by a slight swelling in *Atrichornis* is present on metacarpal II about midway between proximal and distal ends on the external border in *Menura*. The external carpal trochlea in *Atrichornis* extends relatively farther proximally than the internal trochlea, whereas in *Menura* this difference is less pronounced. The intermetacarpal tuberosity has a narrower base in *Atrichornis* than it has in *Menura*, when viewed externally. The ligamental groove on the external surface of the distal half of the carpometacarpus is deep and well defined in *Menura*, but is shallow and broad in *Atrichornis*.

Femur. In proximal view, *Menura* has a femoral head whose anteroposterior depth is more than one-half of the depth of the trochanter, whereas in *Atrichornis* the depth of the head is no more than half the depth of the trochanter. The neck (viewed proximally) in *Menura* is more emphasized than in *Atrichornis*, mainly because the anterior margin of the proximal end, just lateral to the head, in *Menura* is broadly concave anteriorly, and not narrowly notched as in *Atrichornis*. In medial view, the shaft of the femur in *Atrichornis* is markedly curved, being concave posteriorly, whereas in *Menura* it is quite straight. In *Atrichornis*, the main flexure occurs distal to the proximodistal midpoint of the shaft. In medial view, the internal condyle of *Menura* is more anteroposteriorly compressed than in *Atrichornis*, where the outline of the internal condyle approximates a half circle. In *Atrichornis*, the mediodistal corner of the posterior shaft surface is excavated, concave posteriorly, whereas this area is not excavated in *Menura*. In posterior view, *Atrichornis* has a small, short obturator ridge on the lateral side of the posterior shaft surface that is a continuation of the proximal articular surface. *Menura* has nothing comparable to this, with only a distinct process on the lateral side of the trochanter for muscle attachment, which is also present in *Atrichornis*. In anterior view, the trochanteric ridge of *Menura* is bifurcated with a short ridge medial (that continues into the anterior intermuscular line) to a second ridge, which occurs along the border of the shaft. *Atrichornis* has a single, laterally placed ridge. The lateral trochanteric ridge in *Menura* is basically divided into two parts, a proximal, more massive, and a distal, more delicate section, both separated by a swail. In *Atrichornis*, the two parts of the ridge are developed, but the distal segment is not at all prominent. In *Atrichornis*, the anterior intermuscular line joins the trochanteric ridge along the lateral shaft border, about one-third the shaft's length from the proximal end, and continued as a very slight ridge down the midline of the shaft; in *Menura*, the anterior intermuscular line originates from the medial branch of the trochanteric ridge, in the middle of the shaft near the proximal end, and continues as a prominent ridge angling across the shaft towards the internal border. In lateral view, the most proximal projection occurs at the anterior part of the trochanter in *Atrichornis*. In *Menura*, the proximal-most projection occurs at a point between the anteroposterior midpoint and the border of the shaft. Thus, the shape of the trochanter is different in the two genera. In distal view, the fibular condyle and the external condyle in *Menura* appear to be more inflated and more massive, relative to the internal condyle, than in *Atrichornis*. The rotular groove in *Atrichornis* is nearly bilaterally symmetrical, whereas in *Menura* it is assymmetrical with the deepest part being displaced medially from the mediolateral midpoint. In distal view, the medial margin of the internal condyle in *Atrichornis* is straight and nearly perpendicular to the mediolateral axis of the distal end. In *Menura*, although also straight, the medial margin of the internal condyle forms an obtuse angle with the distal ends of the axis; thus, the posterior edge of the internal condyle extends further, medially, than the anterior edge.

Tibiotarsus. In proximal view, the inner cnemial crest of *Atrichornis* is near the internal side of the proximal end, while in *Menura* the crest is displaced externally nearing the midline. In *Atrichornis*, the inner cnemial crest protrudes only slightly beyond the anterior border of the proximal end, whereas in *Menura* the crest extends far anteriorly. The inner cnemial crest in *Menura* also extends far beyond the proximal articular surface. In *Atrichornis*, the crest does not extend far proximally. In proximal view, the interarticular area at the base of the cnemial crest is marked by two moderately deep depressions in *Atrichornis*. In *Menura* these are relatively shallower. The ligamental attachment distal to the inner cnemial crest originates at the base of the crest in *Atrichornis*, whereas in *Menura* it is further displaced, extending distally to the level at which the fibular crest begins. In *Atrichornis*, the ligamental crest terminates before the fibular crest originates on the opposite side of the shaft. Thus, the ligamental crest is separated by a gap from the inner cnemial crest in *Menura*, whereas it merges with that crest in *Atrichornis*. The fibula in some *Menura* is more elongate with respect to the shaft than in the *Atrichornis* studied, where the fibula extends slightly beyond the fibular crest. This character, however, seems to be a most variable one even on opposite sides within the same bird. On NMV B10730, the left fibula, which appears to be complete, extends only 16.5 mm beyond the distal end of the fibular crest, whereas the right fibula is elongate, extending 40.5 mm beyond the fibular crest (in *Menura*). In anterior view, the shaft surface medial to the fibular crest is marked by a distinct ridge running distomedially from the lateral margin in *Menura*. This

Plate V. Wing elements of *Menura*. B, C, E, G, I, K, N, O, Q: *M. novaehollandiae* (NMV W8713); A, D, F, H, J, L, M, P, R, *M. alberti* (AM S593). A, B: humeri, proximal view; C, D: humeri, distal view; E–F, I–J: humeri, anconal view, stereo pair; G, H: radii, palmar view; K, L: radii, anconal view; M, N: humeri, ventral view; O–R: humeri, palmar view, stereo pairs. Scales = 10 mm; single scale applies to E–R .

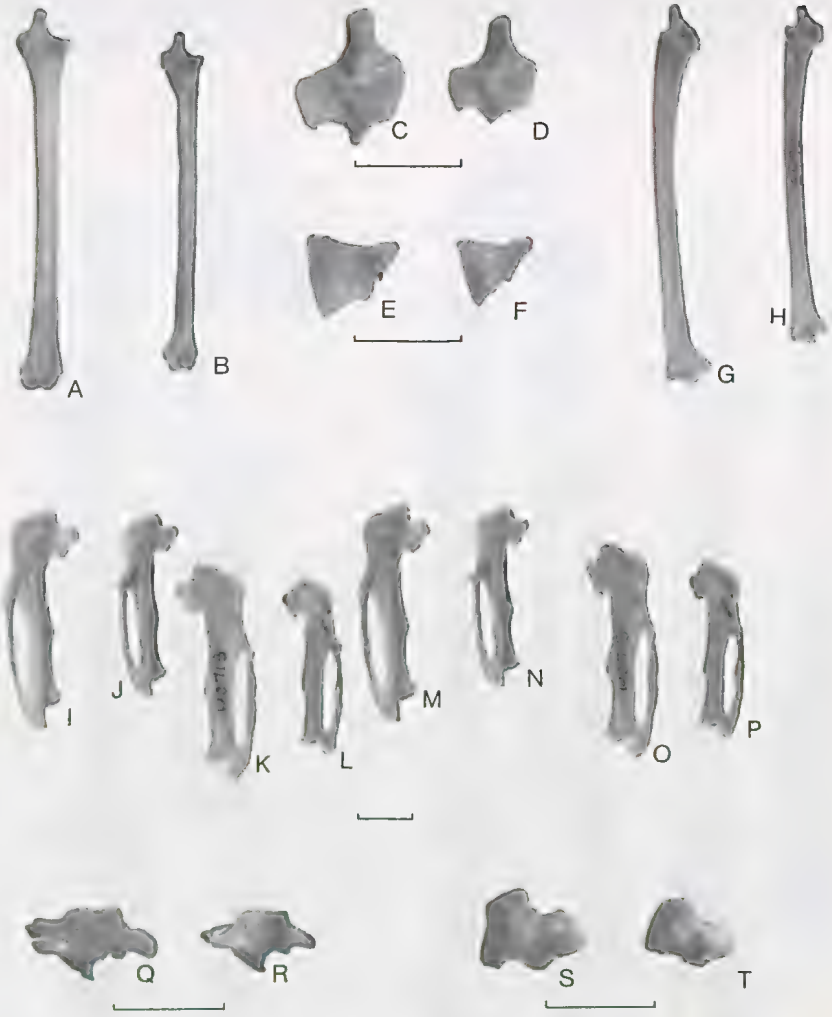

Plate VI. Wing elements of *Menura*. A, C, E, G, I, K, M, O, Q, S: *M. novaehollandiae* (NMV W8713); B, D, F, H, J, L, N, P, R, T: *M. alberti* (AM S593). A, B: ulnae, anconal view; C, D: ulnae proximal view; E, F: ulnae, distal view; G, H: ulnae, palmar view; I–J, M–N: carpometacarpi, internal view, stereo pairs; K–L, O–P: carpometacarpi, external view, stereo pairs; Q, R: carpometacarpi, proximal view; S, T: carpometacarpi, distal view. Scales = 10 mm; same scale applies to A–B, G–H, I–P.

Plate IX. Hind limb elements of *Menura*. A, C, E, G: *M. novaehollandiae* (NMV W8713); B, D, F, H: *M. alberti*. A–D: anterior view, including metatarsal I, stereo pairs; E, F: internal view; G–H: distal view. Scales = 10 mm. Single scale applies to A–F; single scale applies to G–H.

Plate VIII. Femora of *Menura*. A, C, E, G, I, K, M: *M. novaehollandiae* (NMV W8713); B, D, F, H, J, L, N: *M. alberti* (AM S593). A–D: anterior view, stereo pairs; E, F: lateral view; G–J: posterior view, stereo pairs; K, L: medial view; M, N: proximal view. Scales = 10 mm. Single scale applies to A–L; single scale applies to M–N.

Plate X. Tarsometatarsi of *Menura*. A, C, E, G: *M. novaehollandiae* (NMV W8713); B, D, F, H: *M. alberti* (AM S593). A–D: anterior view, including metatarsal I, stereo pairs; E, F: internal view; G, H: distal view. Scales = 10 mm. Single scale applies to A–F; single scale applies to G–H.

Plate XI. Tarsometatarsi of *Menura*. A, C, E: *M. novaehollandiae*; B, D, G: *M. alberti*. A–D: posterior view, including metatarsal I, stereo pairs; E–G: lateral view. Scale = 10 mm.

ridge is totally lacking in *Atrichornis*. In *Atrichornis*, the shaft surface is gently rounded. The posterior intercondylar sulcus is deeply excavated in *Menura* — only shallowing so in *Atrichornis*. In *Menura*, when viewed distally, a distinct ridge is present within the intercondylar sulcus, located slightly lateral of the midpoint, and this is much less pronounced in *Atrichornis*. In medial view, the rim of the internal condyle in *Atrichornis* is flattened distally, not rounded as in *Menura*. In external view, in *Menura* the ridge along the distal part of the shaft leads into the external ligamental prominence, which is quite distinct. In *Atrichornis* neither ridge nor prominence is present.

Fibula. In lateral view, the proximal end of the fibula of *Menura*, on the anterior half of the shaft, rises more abruptly from the fibular shaft and presents a better defined surface of ligamental attachment than in *Atrichornis*, where this area is relatively smoother. In side view, the fibula of *Atrichornis* tapers gradually toward its distal end; but in *Menura* this bone tapers abruptly about midway along the fibular attachment to the tibiotarsus to produce a flattened, splint-like, knife-edged bone over the remainder of its length. In proximal view, the head of the fibula is concave on the internal side in *Menura* and is nearly straight in *Atrichornis*.

Tarsometatarsus. *Atrichornis* has three tendinal canals; *Menura* has five. The shapes of the proximal articular surfaces differ in the two genera, *Menura* being more expanded anteroposteriorly on the external and internal margins, thus being dumbell-shaped; *Atrichornis* has a more rectangular-shaped surface. In both genera a ridge or process, perhaps more properly termed a calcaneal ridge, extends far posterior to the external cotyla, ending between the first and second calcaneal canals. In *Atrichornis* the ridge is decidely shorter than that in *Menura* with respect to width of the proximal end. In *Menura*, the intercotylar prominence occupies all of the space between the anterior and posterior margins of the proximal end, whereas in *Atrichornis* the prominence is restricted to the anterior half of the proximal end. The internal cotyla is more deeply excavated in *Atrichornis* than in *Menura*. In *Atrichornis* the internal margin of the internal cotyla extends farther proximally than the external margin of the external cotyla, yet not as far as the tip of the intercotyla prominence; in *Menura* the margins of the cotylae extend about an equal distance proximally, while the intercotylar prominence extends farther than both. The posterior metatarsal groove is fairly shallow, if present at all in *Atrichornis*. It is located along the more proximal points of the posterior shaft in *Atrichornis*, whereas in *Menura* it is always well developed over most of the shaft. The external ligamental ridge that courses along the posterior surface of the shaft expands relatively farther posteriorly in *Menura* than in *Atrichornis*. Although lower, the ridge extends farther along the shaft in *Atrichornis* than in *Menura*, coarsing well beyond the midpoint in the former and about to the midpoint in the latter. The distal end of the tarsometatarsus in *Menura* tends to expand and broaden more, particularly externally, than in *Atrichornis*; in fact, in *Atrichornis*, the external shaft margin continues nearly as a straight line right into the distal end, not curving laterally. In distal view, the trochlea for digit II in *Menura* is the largest (in surface area) of all the trochleae, followed by III and IV. In *Atrichornis*, trochleae II and III are equal in area, both being distinctly larger than IV. In anterior view of the distal end, the marked depressions occurring at the bases of the trochleae for digits II, III and IV vary as follows: *Atrichornis* — II, a deep depression occurs on the external half of the base; III, the groove ends in a depression; IV, no depression is present. *Menura* — II, a slight depression lies external to centre of the base; III, the groove ends in a deep, central depression at its base; IV, the groove ends in a deep, central depression. In *Menura*, a well developed ossified tendon lies closely apposed to the tarsometatarsus over most of the length of the posterior metatarsal groove; it is flattened over much of its length, but swells to a bulbous distal end that lies external to the proximal end of metatarsal I. We have not observed this in any of the *Atrichornis* specimens available to us.

Osteological Comparisons of *Menura novaehollandiae* and *Menura alberti*

Plates I–XI

Menura novaehollandiae differs from *M. alberti* in having: **Cranium:** greater inflation of the region dorsal to the foramen for the greater mandibular nerve (for n. max. mand.). **Rostrum:** the palantines more proximodistally elongate and laterally compressed. **Sternum:** a marked ventral bulge in the ventral manubrial spine, which is totally lacking in *M. alberti*; deep excavations in the ventral surface on either side of the midline that are quite shallow in *M. alberti*. **Synsacrum:** a proportionally much broader, shorter synsacrum; a relatively larger surface area of the antitrochanter; a relatively shorter ilioischiatic fenestra that is more approaching a circle than ellipsoid in shape; posterior projections of ilium that are relatively wider. **Scapula:** the blade of the scapula more broadly expanded distally (in *M. alberti* the blade tapers to a narrow end gradually, not abruptly); the area between the furcular articulation and the coracoidal atriculation relatively broader in proximal view (this area is more constricted in *M. alberti*), and the furcular articulation relatively shallower in *M. novaehollandiae*. **Coracoid:** better developed sternocoracoidal processes — the lateral border of the shaft abruptly turns externally near the distal end, forming a distinct, well defined process (in *M. alberti* the lateral border grades evenly to the distal end); a brachial tuberosity that forms a smaller acute angle with a long axis of the coracoid in posterior view; the sternal facet not as anteroposteriorly expanded, particularly medial to the mediolateral midpoint; a less deeply excavated dorsal end particularly

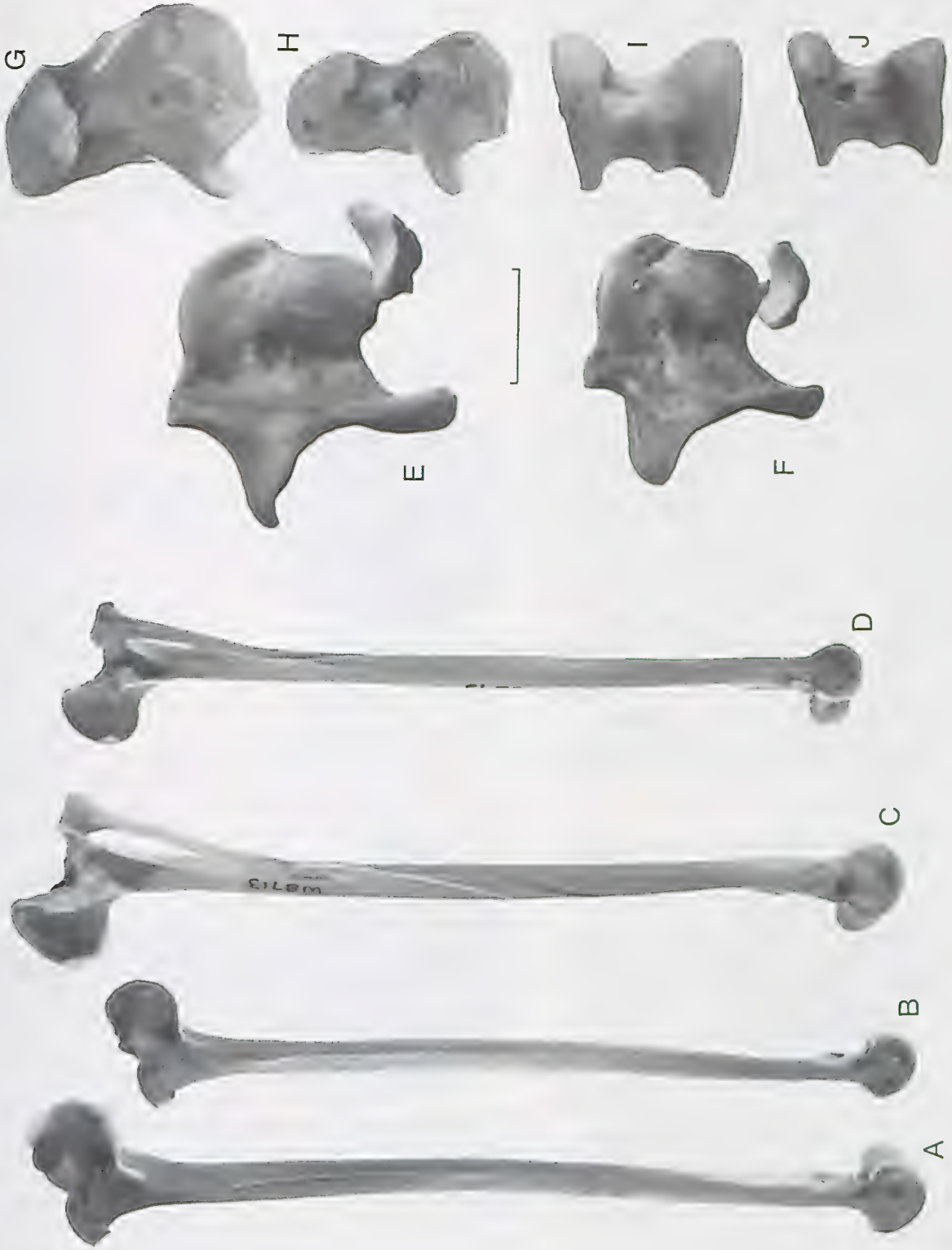

Plate VII. Hind limb elements of *Menura*. A, C, E, G, I: *M. novaehollandiae* (NMV W8713); B, D, F, H, J: *M. alberti* (AM S593). A, B: tibiotarsi, medial view; C, D: tibiotarsi, lateral view; E, F: tibiotarsi, proximal view; G, H: femora, distal view; I, J: tibiotarsi, distal view. Scales = 10 mm. Single scale applies to A–D; single scale applies to E–J.

beneath the furcular facet in posterior view. **Clavicles:** the dorsal end of the clavicles, in side view, more broadly expanded; the coracoidal facet with a greater surface area relative to the size of the entire clavicle. **Humerus:** the deltoid crest better developed and extending distinctly further palmarly; a bicipital surface more inflated, extending relatively further anconally. **Radius:** the distal end somewhat more inflated. **Ulna:** the secondary papillae more prominent. **Carpometacarpus:** the facet for digit III not as squared off but more pointed in internal view; the excavation at the base of the carpal trochleae on the external surface relatively shallower with only a slight impression present; the facet for digit II with an internally directed process that is lacking in *M. alberti* — the facet is also broader, not so mediolaterally compressed in distal view. **Femur:** the internal condyle more anteroposteriorly compressed and proximodistally elongate; the internal condyle more deeply excavated. **Tibiotarsus:** the fibular crest less elongate relative to the total length of the tibiotarsus (13.4–13.5% vs 16.1%), as is the ligamental attachment along the internal side of the bone; the inner cnemial crest extending relatively further proximally; the external ligamental prominence pronounced, not inconspicuous. **Fibula:** the variability between individuals of *M. novaehollandiae* is quite marked and sufficient to account for differences seen between specimens of *M. novaehollandiae* and *M. alberti*. **Tarsometatarsus:** the anterior border of the proximal end not as deeply incised, thus making the cotylae project less abruptly forward in proximal view; five tendinal canals (*M. alberti* has six); the medial border of the outer calcaneal ridge not straight, but notched, unlike that in *M. alberti*; there are no apparent differences in the distal ends of the tarsometatarsi in the above two species. Note: The internal edge of the bone (upper region) is more decidedly flattened in *M. alberti*.

Osteological Comparisons of *Atrichornis clamosus* and *Atrichornis rufescens*

Plates XII-XIX

Atrichornis clamosus differs from *A. rufescens* in being: **Sternum:** more elongate with respect to width, i.e., more slender; in having: a relatively narrow ventral manubrial spine that is only slightly, not broadly, bifurcated; a more anteroposteriorly elongated ventral manubrial spine that extends anteriorly from the main body of the sternum nearly half of the length of the sterno-coracoidal process, instead of about ⅓ the length; a carina that is, although shallow, still deeper than that in *A. rufescens*, and that grades into the main body of the sternum posteriorly, not expanding abruptly ventral near its anterior end; a sternum that is more highly concave dorsally, not flattened.

Atrichornis clamosus differs from *A. rufescens* in having: **Synsacrum:** a somewhat narrower anterior half with the bony surface of the ilium either side of the median ridge more vertically oriented; more flexure between the front and back halves of the synsacrum (when viewed laterally); a relatively narrower and more elongate ishiopubic fenestra; a more anteroposteriorly elongated ischium that narrows abruptly, rather than gradually, near the connection with the pubis; a relatively large obturator foramen, nearly the size of the acetabulum, instead of decidedly smaller; pubes that don't flare broadly, thus making the entire synsacrum narrower posteriorly. **Scapula:** a slender and elongate process along the dorsal border of the proximal end between the furcular articulation and the glenoid facet (in *A. rufescens* this process is short and broad); a very distinct and well defined furcular articulation instead of one that merges gradually with the rest of the proximal articular surface; a furcular facet that is well defined and separate from the rest of the proximal end, and does not evenly grade into it in proximal view; a furcular articulation whose lateral margin forms a smaller obtuse angle with the glenoid facet than in *A. rufescens*, when viewed dorsally; a more rounded apex. **Coracoid:** a proportionally shorter internal surface of the shaft, just distal to the procoracoid groove; a slightly more prominent procoracoid; a sternal facet only moderately concave, not highly concave ventrally in anterior or posterior view; a straight, rather than convex, lateral margin of the coracoid near the distal end. **Humerus:** (Only proximal ends available for comparison) a distinctly larger humerus; a deep excavation at the base of the capital groove that is lacking in *A. rufescens*, in anconal view; a relatively more prominent internal tuberosity; a much more deeply excavated pneumatic fossa; a better developed, more elongate, deltoid crest; a proximal end that is broadly, not just slightly, splayed, where the bicipital surface extends relatively further internally; a distinct ridge on the external surface of the shaft at the base of the deltoid crest that is totally lacking in *A. rufescens*. No more distal wing elements are preserved in our collections of *A. rufescens*.

Femur: the most proximal extension of the trochanter occurring near its anterior end rather than near the anteroposterior midpoint; a shallow, not deep, excavation on the proximal end of the shaft's posterior surface near the base of the trochanter; when viewed laterally, it lacks a deep notch in the posterior shaft border near the proximal end; when viewed proximally, the head shifted further posteriorly with respect to the trochanter, extending further posteriorly than the trochanter itself, and with the head extending relatively further internally, possessing a more elongate neck; a much more highly curved shaft (concave posteriorly); a relatively more deeply excavated anterior shaft surface at its proximal end. **Tibiotarsus:** a rotular crest that is both lower and rises more gradually from the articular surface; an outer cnemial crest (in anterior view) that ends in an apex rather than being blunt and rounded; a very prominent ligamental attachment on the posterointernal surface of the shaft near the proximal

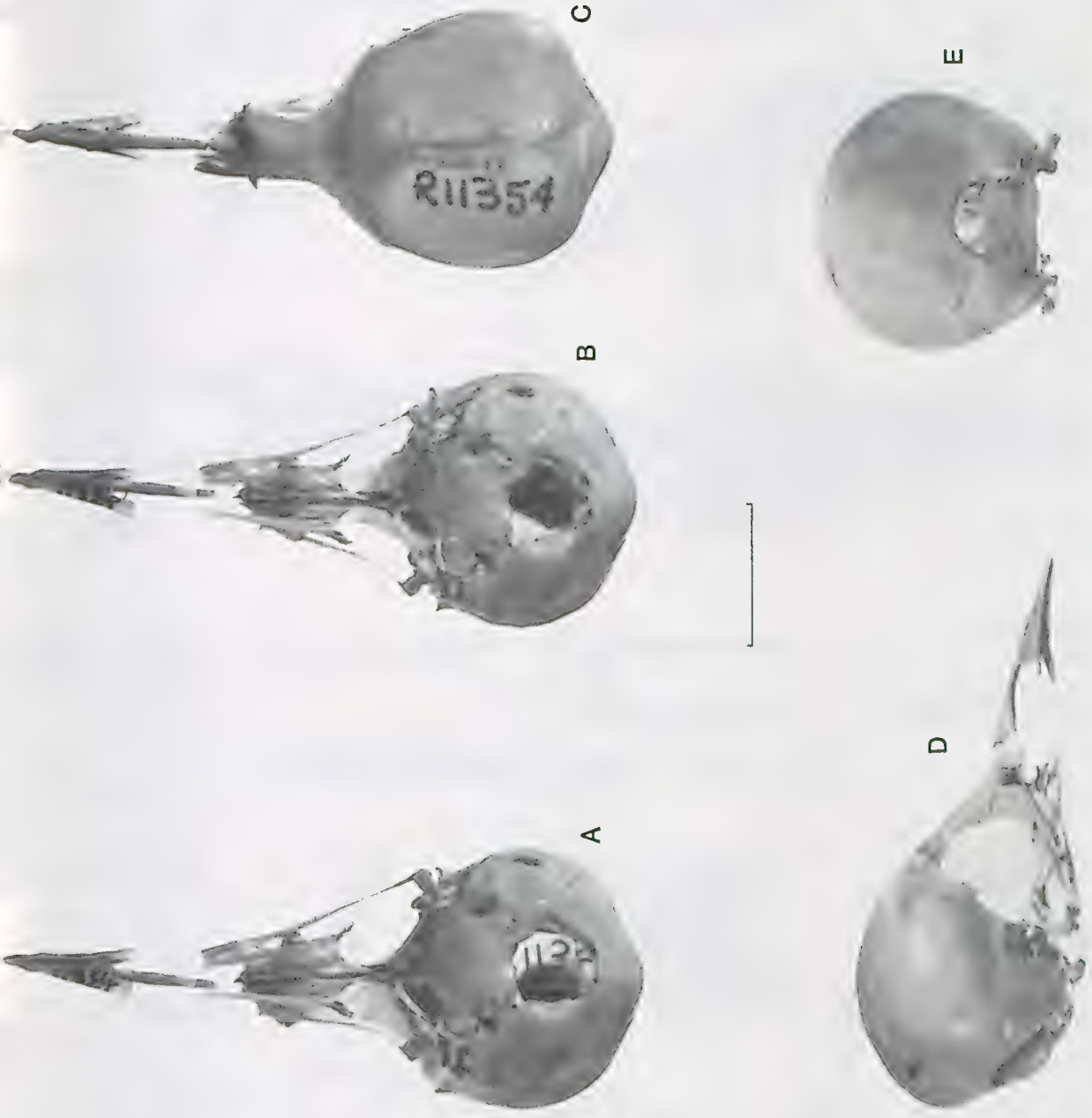

Plate XII. Skull of *Atrichornis clamosus* (NMV R11354). A–B: ventral view, stereo pairs; C: dorsal; D: lateral; E: posterior views. Scale = 10 mm.

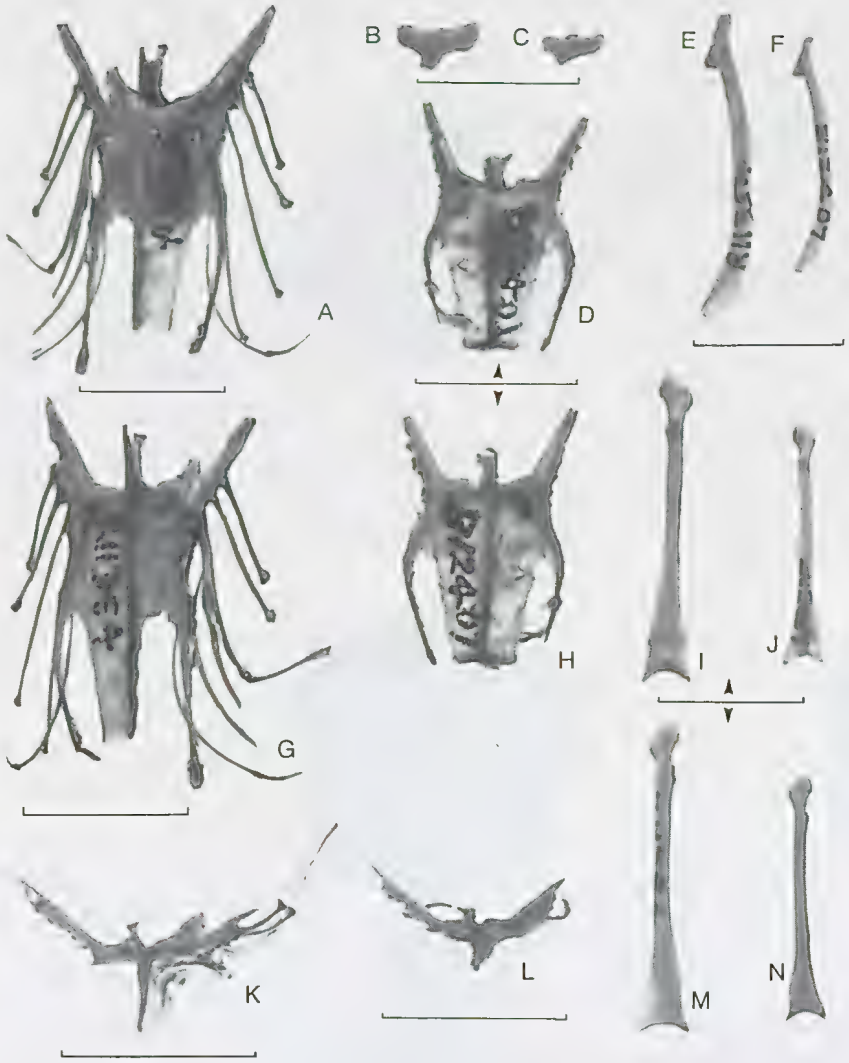

Plate XIII. Sterna and shoulder girdle elements of *Atrichornis*. A, B, E, G, I, K, M: *A. clamosus* (NMV R11354); C, D, F, H, J, L, N: *A. rufescens* (NMV B12407). A, D: sterna, dorsal view; B, C: scapulae, distal or articular view; E, F: scapulae, dorsal view; G, H: sterna, ventral view; I, J: coracoids, internal view; K, L: sterna, anterior view; M, N: coracoids, external view. Scales = 10 mm.

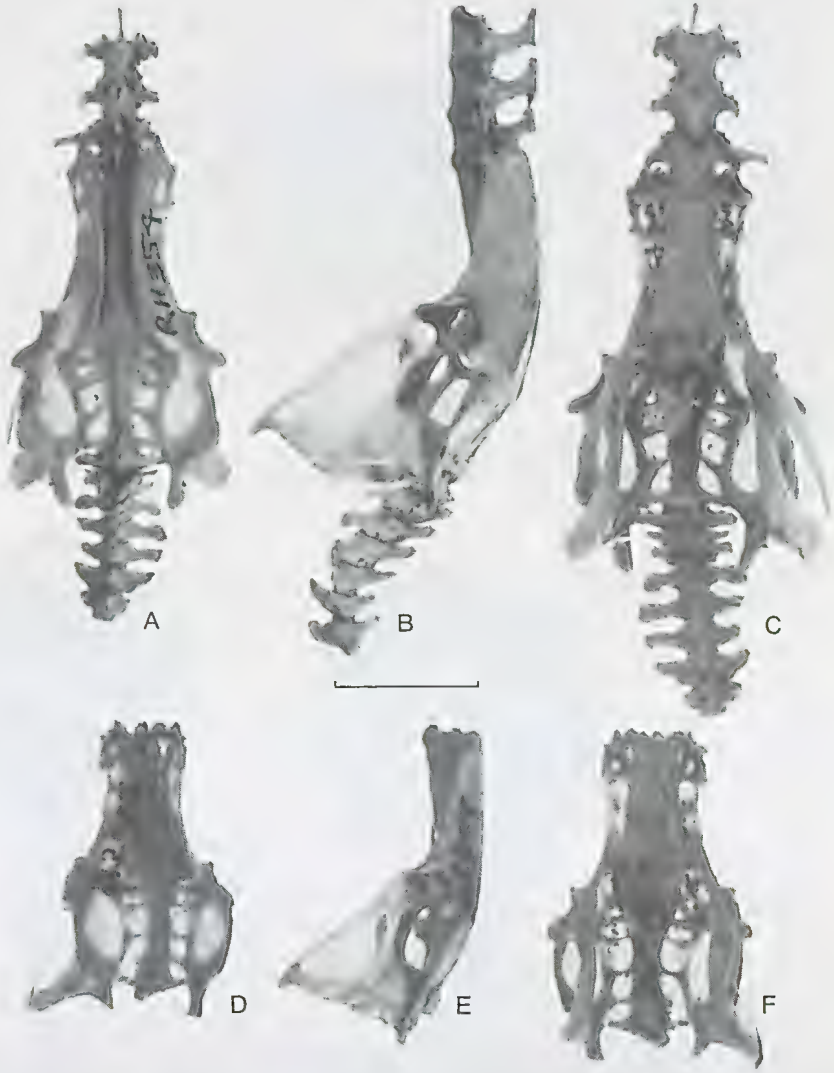

Plate XIV. Synsacra of *Atrichornis*. A–C: *A. clamosus* (NMV R11354) D–F: *A. rufescens* (NMV B12407). A, D: dorsal; B, E: lateral; C, F: ventral views. Scale = 10 mm.

Plate XV. Wing elements of *Atrichornis*. A, C, D–H, J, K, M, N, P–U, W, Y, Z: *A. clamosus* (NMV R11354); B, I, L, O, V, X: *A. rufescens* (NMV B12407). A, B: humeri, proximal view; C: humerus, distal view; D: ulna, anconal view; E, ulna, palmar view; F: ulna, proximal view; G: carpometacarpus, proximal view; H, I: proximal humeri, ventral view; J: distal humerus, external view; K–L, N–O: proximal humeri, palmar view, stereo pairs; M, P: carpometacarpi with attached phalanges, internal view, stereo pair; Q, S: distal humerus, palmar view, stereo pair; R, T: distal humerus, anconal view, stereo pair; U–X: proximal humeri, anconal view, stereo pairs; Y: carpometacarpus, external view; Z: articulated ulna, radius, carpometacarpus and phalanges, external view. Scales = 10 mm. Single scale applies to A–Y; single scale applies to Z.

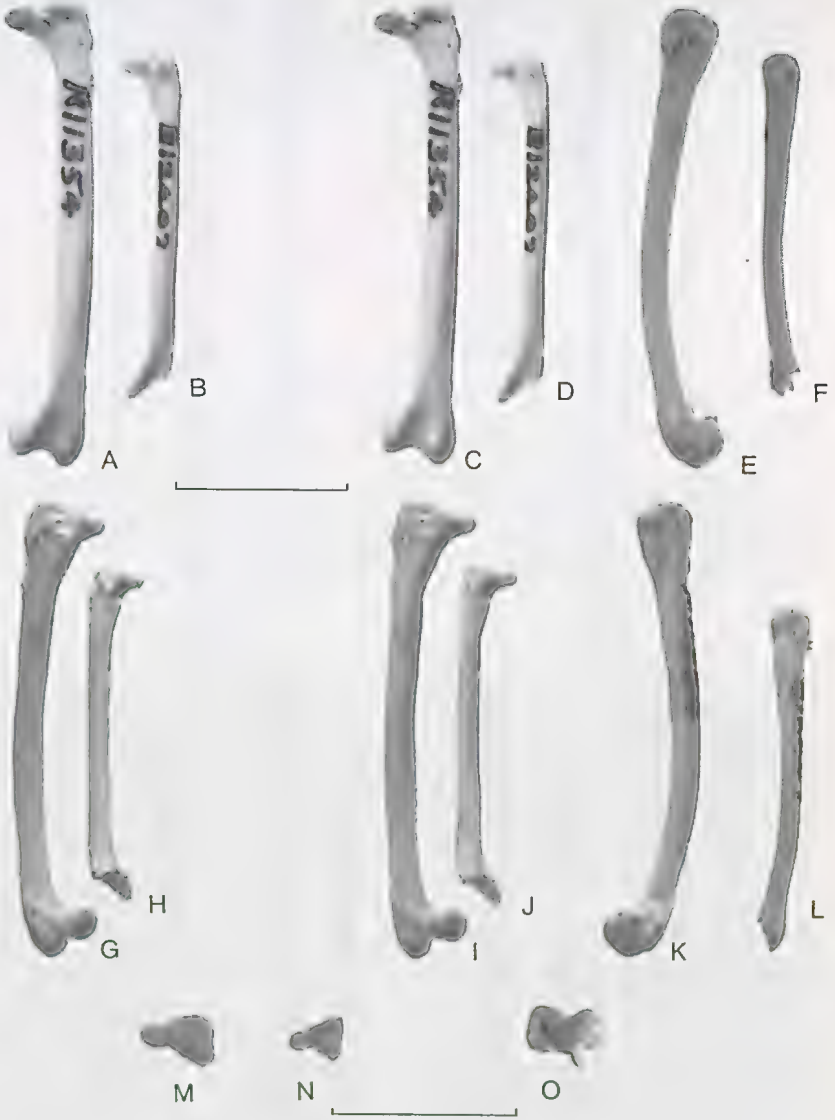

Plate XVI. Femora of *Atrichornis*. A, C, E, G, I, K, M, O: *A. clamosus* (NMV R11354); B, D, F, H, J, L, N: *A. rufescens* (NMV B12407). A–D: anterior view, stereo pairs; E, F: lateral view; G–J: posterior view, stereo pairs; K, L: internal view; M, N: proximal view; O: distal view. Scales = 10 mm. Single scale applies to A–L; single scale applies to M–O.

end; a more distally flattened internal condyle; a posteriorly flattened external condyle, not one that is smoothly rounded. **Tarsometatarus:** the hypotarsus is not well preserved, but it appears that *Atrichornis clamosus* differs from *A. rufescens* in having: 3 hypotarsal canals rather than 1; no distinct groove on the posteroexternal border of the hypotarsus behind the hypotarsal canal on that side; an external cotyla (viewed proximally) with a flattened, straight, anterior/external corner, not a smoothly rounded margin; a broadly splayed proximal end (in anterior or posterior view); trochleae that are more nearly the same length (in *A. rufescens* trochlea IV is decidedly shorter than trochlea II and III).

Discussion

In our study of the skeletons of *Atrichornis* and *Menura*, comparisons have not clearly resolved the relationships of these birds. What the study has illustrated, for the first time osteologically, is the close similarities between the two species of *Menura* and between the two species of *Atrichornis* clearly illustrated in the plates, not a startling discovery. Most of the differences between each species in the pairs (which are enumerated in the text) are minor proportional ones, and many are likely correlated with reduction in flying ability. *Menura novaehollandiae*, for instance, has osteological characteristics that would suggest it is a stronger flier than *M. alberti* in having a better developed deltoid crest on the humerus and a better developed sternum with a greater surface area per unit length (both areas of flight muscle attachment), as well as better developed secondary papillae on the ulna for secondary feather attachment. Likewise, *Atrichornis clamosus* appears to be more 'volant' than *A. rufescens* in having a better developed deltoid crest (= pectoral crest) on the humerus and a better developed sternum with a deeper keel. Differences in the hind limbs of these species pairs remain unexplained functionally at the moment until field studies may allow better understanding of behavioural traits.

On the other hand, as illustrated in the section on osteological comparison of *Menura* and *Atrichornis*, there are many differences between these genera. Some differences, again, can be directly correlated with the greater reduction of flying ability in *Atrichornis*: this species has a reduced coracoid and sternum; extremely reduced clavicles, so that only two slender spikes are retained that do not fuse to form a furcula; a reduced deltoid crest on the humerus; decidedly reduced feather papillae on the ulna; and a reduced and extremely shortened and broadened carpometacarpus. Differences, too, exist in the hind limb and synsacrum, but what these mean functionally at this stage is uncertain.

In order to complete the taxonomic evaluation of their osteology, comparisons with members of each of the passeriform families and those in the 'higher' non-passeriforms, such as Coraciiformes and Piciformes, are underway. Feduccia (1975 a, b) has already carried out such a study on the columella, but many other osteological characteristics need to have similar evaluations. This is, of course, necessary if any attempt is to be made to determine the primitive or advanced nature of each of these individual characteristics. Only then, such differences as the presence of three or five hypotarsal canals on the tarsometatarsus, the presence or absence of a bony bridge on the tibiotarsus, or the degree of flexure of the synsacrum can be evaluated in light of the entire passeriform assemblage.

During such evaluations across the order Passeriformes, the possibility of convergence due to similarity of lifestyle must constantly be kept in mind. Many of the characters mentioned by Feduccia & Olson (1982) that link *Atrichornis* and *Menura*, and both of these genera in turn to some Rhinocryptidae, are features that repeatedly occur in a wide variety of terrestrially adapted passeriforms, many of which have never been considered to be phylogenetically close (e.g. *Menura* and *Callaeus*; see Table 2). So the question arises whether these characters were derived only once in their common ancestry or are merely a complex of derived characters associated with increased cursoriality and, therefore, convergent.

Let us take specific examples from Table 2 to exemplify this. We will consider non-passeriforms first and then passeriforms. One of the elements most affected by decreased volancy is the humerus. As Olson (1973) states: "In my opinion, the energy factor is the overriding consideration in the evolution of flightlessness". Energetically, it is most useful to remove appendages which no longer function as necessary structures. This is well demonstrated in the rails. The statement that "flightlessness in rails can probably be measured in generations rather than millenia" (Olson, 1973) implies that it is useful for birds to remove unnecessary structures quickly, when possible. Rails have the ability to lose their power of flight rapidly, because the long bones, sternum, and girdles are not fully ossified post-hatching and, therefore, environment can play a key role in the moulding of a bird's habits (Olson, 1973). As it seems rails can lose their ability to fly rapidly, we can compare the humeri between volant and non-volant forms within the same rallid genus. In *Gallinula*, for example, there are two closely allied forms, *G. mortierii* and *G. ventralis*: the first is flightless, the second is fully volant. In the humerus of *G. mortierii* the length is equal to that of its congenor, whose body size is half as large, so a comparative shortening has occured. The reduction in the pectoral appendage in *Atrichornis* and *Menura* has also been noticed by Raikow (1985). In addition to overall reduction, the proximal end of the humerus is tilted medially, with respect to the body, an action which brings the capital groove in line with the long axis of the shaft. The tilting also brings the internal tuberosity almost level with the proximal part of the head. The pectoral crest is rotated dorsomedially with respect to the shaft, but this character is not as diagnostic for the

Plate XVII. Hindlimb elements of *Atrichornis*. A, B, D, E, G, H, J, L, N, O, Q, S, U: *A. clamosus* (NMV R11354); C, F, I, K, M, P, R, T, V: *A. rufescens* (NMV B55794). A–C: tibiotarsi, proximal view; D: tibiotarsus, external view; E, F: tibiotarsi, internal or medial view; G–I: tibiotarsi, posterior view; J, K: tarsometatarsi, internal view; L, M: tarsometatarsi, lateral or external view; N–P: tibiotarsi, internal view; Q, R: tibiotarsi, distal view; S, T: tarsometatarsi, proximal view; U, V: tarsometatarsi, distal view. Scale = 10 mm.

Plate XVIII. Hindlimb elements of *Atrichornis*. A, B, D, E, G, I, K, M: *A. clamosus* (NMV R11354); C, F, H, J, L, N: *A. rufescens* (NMV B55794). A–F, tibiotarsi, anterior view, stereo pairs; G–J, tarsometatarsi, anterior view, stereo pairs; K–N, tarsometatarsi, posterior view, stereo pairs. Scale = 10 mm.

Rallidae. The shaft is curved and stout with respect to that of *G. ventralis*. The same description was given by Olson (1973) for the humerus of flightless rails of the Atlantic, and by Olson & Wetmore (1976) and Olson & Steadman (1979) for two species of flightless ibises. Olson & Steadman (1979) mentioned that the humerus is useless for taxonomic characters, and yet in Feduccia & Olson (1982) this same shaped humerus is used for the alliance of Menurae and rhinocryptids. So, why aren't the same criteria producing the same conclusions for the Passeriformes? The abovementioned characters can be explained by a decreased use of the wings, as can be seen in modern songbirds (e.g. *Dasyornis, Amytornis, Callaeas*), and so use of such characters in determining phylogenetic similarity is rather unwise unless supported by other data.

The sternum may also be considered to be a good measure of the bird's flight capabilities. Figure 1 shows the sternal outlines of the passeriforms *Menura*, *Atrichornis*, *Dasyornis, Amytornis* and *Callaeas* in lateral view, as compared with volant forms, *Malurus* and *Philemon*. The sternal keel can be seen as to be much reduced in the first group as compared with the second, a character which Olson (1973) also pointed out as being a measure of flightlessness.

With a decreased use of the wings the emphasis on the legs occurs. This is reflected in the clambering arboreal existence of *Callaeas* (Falla, Sibson & Turbott, 1981) or a terrestrial/cursorial mode of life in *Dasyornis* and *Amytornis* (Pizzey, 1980; Schodde, 1982). The increased use of the hindlimb in a terrestrial sense is reflected by corresponding changes in each of the three long bones composing this limb (e.g. increased size of the trochanteric ridge of the femur; emphasis of a ridge between the distal trochlea on the tibiotarsus; and lateral expansion of the trochlea on the tarsometatarsus, among others.) All of these characters can be seen on the aforementioned genera. The presence of the sulcus on the third (outer) trochlea on the tarsometatarsus is related to the degree of use of the feet in foraging, as well as in locomotion. This condition is well developed in the genus *Menura* (Smith, 1968).

Special structures mentioned by Feduccia & Olson (1982) not correlated with terrestriality could be used in phylogenetic reconstructions, but, unfortunately, like the ossified ridge of the culmen of *Atrichornis* and some rhinocryptids, many of these can also be found in other taxa. At least two species of friarbirds (*Philemon argenticeps* and *P. corniculatus*) bear an ossified ridge on the culmen, although admittedly, it is swollen as compared with *Atrichornis*. In *Philemon*, a genus of meliphagid, the culmen ridge is present in these two species, but lacking in a third, *P. citreogularis*. Another special structure is the notch and knob arrangement of the two outer basal tarsal phalanges. But this, once again, is a character probably associated with cursoriality and found also in *Cinclosoma*, a genus presently placed in the Orthonychidae, most probably a polyphyletic group. According to Sibley & Ahlquist (in press), *Cinclosoma* probably belongs within the superfamily Corvi.

Why haven't many of these characters previously been associated with terrestriality in passeriforms? The problem is twofold: first, many of the non-volant or semi-volant birds relying on laboured flight or gliding occur in the Southern Hemisphere and are rare in museum collections. Often they occur only in their respective countries of origin, where only a few, if any, workers might have an interest in classical taxonomy. Secondly, within their respective groups, each of the genera exhibiting characters of 'semi-flightlessness' are the extreme of a range of morphologies within the family. For example, the genus *Amytornis*, according to Schodde (1982), belongs in the family Maluridae with four other genera, *Stipiturus*, *Malurus, Clytomyias* and *Sipodotus*.

Malurus is a genus characterised by its bright array of brilliant blues, reds and purples and spends most of its time moving in closely knit family groups in the scrub layer. The postcranial elements of these birds are of volant birds, with large, straight pectoral crests, humeral heads posterodistally projecting, etc. *Amytornis*, in contrast, consists of generally drab brown or black birds that also move about in closeknit family groups but are mostly confined to the arid inland, spending much of their time either on the ground or in clumps of Porcupine Grass (*Triodia* sp.). The flight of *Amytornis* is laboured and rarely observed (Schodde, 1982). Therefore, it would be expected to have just the type of humerus that it indeed has, that of a non-volant or semi-volant bird. Thus, the range of volant vs. semi-volant forms within a family can be quite extreme. Although a good series of rhinocryptids is not available to us, it appears that it may be a group with both cursorial and volant forms with varied stages in between. Into a sequence such as this, the stages attained by *Atrichornis* and *Menura* can be slotted quite easily. The fact that these two genera have forms intermediate between them in the rhinocryptids, based on the characters discussed by Feduccia & Olson (1982), however, does not yet support close relationship of any of these groups. More information is needed before that decision can be made.

Summary and Conclusions

Detailed comparisons of the postcranial skeleton of all species of *Atrichornis* and *Menura* confirm that the two species of *Menura* are indeed closely related, as are the two species of *Atrichornis*. Not so clear, however, are the relationships of *Menura* to *Atrichornis*. Although they share simple syringes, they also show a number of differences in detail of the syringeal muscles (e.g. *Atrichornis* has short ventral muscles, while *Menura* has none) and in morphology and degree of fusion of the tracheal rings. Both genera possess a primitive avian stapes and lack the expanded bulbous footplate that characterizes the derived suboscines.

Plate XIX. A comparison of the skeletons of *Menura novaehollandiae* (NMV B10730) and *Atrichornis clamosus* (NMV R11345). A, C, F, G, J, L, N, P, R, T, V: *M. novaehollandiae*; B, D, E, H, I, K, M, O, Q, S, U, W: *A. clamosus*. A, pelves and synsacra; C, D: sterna; E, F: shoulder girdles (E, includes silver-like clavicle, coracoid and scapula; F, clavicles only); G, H, I: humeri; J, K: ulnae; L, M: carpometacarpi; N, O: femora; P, Q: tibiotarsi; R, S: coracoids; T, U: scupulae; and V, W: tarsometatarsi. Scale = 10 mm.

Volancy	*Rhynochetos* (Rhynochetidae) NV	Rhinocryptidae SV	*Pitta brachyura* (Pittidae) V	*Menura novaehollandiae* (Menuridae) V	*Atrichornis* (Atrichornithidae) SV	*Orthonyx temminckii* (Orthonychidae) V	*Cinclosoma* (Orthonychidae) V	*Philemon argenticeps* (Meliphagidae) V	*Amytornis* (Maluridae) SV	*Dasyornis* (Acanthizidae) V	*Callaeas* (Callaeidae) —	Meliphagidae V
External Resemblances												
1. long, strong front and hind claws	—	✓	✓	✓	✓	✓	—	—	—	—	—	—
2. external nasal operculum	✓	✓	—	✓	✓	✓	✓	✓	✓	✓	✓	✓
Comparative Osteology												
3. osseus ridge of the culmen	—	✓	—	—	✓	—	—	✓	—	—	—	✓
4. sternal notches deep; sternocoracoidal processes very long, attenuate and anteriorly directed	—	✓	—	—	✓	—	—	—	—	—	—	— (some)
5. clavicles unfused	—	✓	—	—	✓	—	—	—	—	—	—	—
6. (A) humerus with a slender, curved shaft, (B) proximal end with distinctive reduced curved deltoid crest, etc. (✓ = A & B)	✓	✓	—	B	✓	—	—	—	B	B	B	—
7. carpii short and stout with broad intermetacarpal tubercle and exceptionally large carpometacarpal process	—	✓	—	✓	✓	✓	—	—	✓	✓	✓	—
8. pelvis with most posterior part of ilium overhanging distally	—	✓	✓	✓	✓	—	✓	✓	—	✓	✓	✓
9. femur with strongly developed lateral trochanteric ridge	—	✓	—	✓	—	✓	—	—	✓	✓	—	—
10. tibia with proximal end offset from line of shaft, and well developed, blade-like crest on internal side of proximal end of shaft	—	✓	—	✓	✓	✓	—	✓	✓	✓	✓	✓ (some)
11. tibia distally with deep intercondylar excavation and particularly well defined ridge within the excavation	—	✓	✓	✓	—	✓	—	✓	✓	✓	✓	✓
12. tarsi with inner and outer trochlea very broad and distinctly grooved	✓	✓	✓	✓	✓	—	—	—	—	—	—	—
13. toes with basal phalanx of digit IV distinctly notched to accommodate knob protruding from basal phalanx of digit III	—	✓	—	✓	✓	—	✓	—	—	—	—	—

Table 2. Distribution, in a select group of non-passerines and passerines, of characters used by Feduccia & Olson (1984) to suggest phylogenetic closeness of the Menurae and Rhinocryptidae. ✓ = character present, — = character absent; v = volant, sv = semi-volant, nv = non-volant.

Primitive character states, however, give little information about relationship, and in this case simply indicate what groups neither *Menura* nor *Atrichornis* belong to. Many of the osteological similarities discussed by Feduccia & Olson (1982) and Raikow (1985) can be explained by convergence towards a terrestrial lifestyle and should be used very cautiously when seeking to determine relationships. Although Raikow (1985) points out that *Atrichornis* and *Menura* possess "a number of distinctive myological conditions not found in any passerine group whose appendicular myology has yet been studied", a study that incorporates a number of representatives of each of the endemic Australasian forms, as well as the whole spectum of passeriform families and a thorough analysis of the effects of flightlessness on myology in different passeriform families, needs to be carried out. The results need to be tabularized and presented so the reader can decide the value of these characters relative to passeriforms as a whole. Once characters that could have resulted from functional convergence can be recognized, then perhaps a better estimate of the relationship of *Menura* and *Atrichornis* can be made. At present we do not believe there is sufficient comparative evidence to support any one hypothesis of relationship, even though the possibilities of relationship posed by Feduccia & Olson are intriguing.

Whether the original passerines were terrestrial forms, a possibility raised by Feduccia & Olson (1982), must also remain a moot point until more information is at hand. It would seem difficult to rederive a volant form from terrestrial birds like *Atrichornis*, because element reduction and alteration have been extreme. But perhaps forms that had not proceeded so far could provide the ancestral terrestrial stock for the perching passerines. Another possibility, however, is that the passeriforms developed in an area of the world where the 'perching bird' niches were not so heavily utilized by coraciiforms and piciforms, such as perhaps Australia, and spread from there into areas, e.g. North America, where they met with competition in the trees, and thus moved into the more terrestrial mode of life. Thus, terrestriality, although perhaps developed early in passeriform history, could have been secondarily and even multiply derived. If ever there is a better early Cainozoic record on the Southern Continents, perhaps a choice of

hypotheses can be made, but for now we do not think a single choice is obvious.

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The Skeletomuscular System of the Feeding Apparatus of the Noisy Scrub-bird, *Atrichornis clamosus* (Passeriformes: Atrichornithidae)

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ABSTRACT. The cranial osteology and the jaw and tongue musculature of *Atrichornis clamosus* are described. Noteworthy are the large, free lacrymal and the distinct dorsal hump or ridge on the basal portion of the maxillary culmen. Aside from the lacrymal, little strong support exists in the cranial osteology for the generally accepted relationship between *Atrichornis* and *Menura*. The considerable differences in skull morphology between these genera are not surprising because of the much larger skull of *Menura*, about three times that of *Atrichornis* in linear measurements. Other than the large, free lacrymal, the skulls of the Menurae differ markedly from those of the bowerbirds, arguing against a close affinity between these two groups. The jaw muscles provide no useful information, at this time, on the possible evolutionary history and the affinities of *Atrichornis*, but the tongue musculature does yield some interesting clues. One feature, partial insertion of the M. trachohyoideus on the ceratobranchiale, is relatively primitive, but one aspect of the hyoid skeleton, lateral flattening of the basihyale, and five features of the tongue musculature are advanced. Most interesting are the vestigial nature of the M. stylohyoideus, a condition otherwise known only in woodpeckers and some meliphagids, and the complete insertion of the M. hypoglossus anterior on the anterior tip of the basihyale, seen also in *Dicaeum*, *Oedistoma*, *Promerops* and a few other passerine birds. These features of the tongue musculature suggest strongly that *Atrichornis* is not primitive among the oscines, but do not, as yet, provide a clear idea of its relationships.

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KEYWORDS: Menurae, Atrichornithidae, *Atrichornis clamosus*, relationships, skeletomuscular system, feeding apparatus.

The purpose of this paper is to provide a description of the skeletomuscular system of the jaw and tongue apparatus of *Atrichornis clamosus*. Some comparisons will be made with the skull of *Menura novaehollandiae*; however, full comparison of the cranial morphology of *Atrichornis* and *Menura* must wait until completion of an ongoing study of the latter genus. The available comparisons will permit a few tentative taxonomic conclusions, but more definite ideas on the evolution and relationships of *Atrichornis* to *Menura* and to other passerine birds based on the anatomy of the feeding apparatus must be deferred until detailed analyses are available.

METHODS

Dissections were made with the aid of iodine staining of the musculature, and using a steroscopic dissecting microscope. All illustrations were drawn directly from the dissections with the aid of a drawing tube attached to the microscope, or traced from projected transparencies of the skull. The skull was cleaned by hand after completion of the dissection of the jaw and tongue muscles.

Identification and nomenclature of the jaw and tongue musculature are based on Bock (ms.). The following abbreviations are used in the figures of the musculature.

	Glands
G a o	Glandula angularis oris
G mand	Glandula mandibularis
G max	Glandula maxillaris
	Ligaments
L j m e	L. jugomandibularis externus

L j m i	L. jugomandibularis internus
L p o	L. postorbitalaris
	Jaw Muscles
M a m e c	M. adductor mandibulae externus caudalis
M a m e r	M. adductor mandibulae externus rostralis
M a m r e l	M. adductor mandibulae externus rostralis lateralis
M a m e r m	M. adductor mandibulae externus rostralis medialis
M a m e r t	M. adductor mandibulae externus rostralis temporalis
M a m e v	M. adductor mandibulae externus ventralis
M a m p	M. adductor mandibulae posterior
M d m	M. depressor mandibulae
M p p q	M. protractor pterygoidii et quadrati
M ps p	M. pseudotemporalis profundus
M ps s	M. pseudotemporalis superficialis
M pt	M. pterygoideus
M pt i a	M. pterygoideus infundibularis anterior
M pt i p	M. pterygoideus infundibularis posterior
M pt l	M. pterygoideus lateralis
M pt m a	M. pterygoideus medialis anterior
M pt m p	M. pterygoideus medialis posterior
M pt r	M. pterygoideus retractor
	Tongue Muscles
M b m	M. branchiomandibularis
M b m p	M. branchiomandibularis anterior
M b m a	M. branchiomandibularis posterior
M c c	M. cucullaris caput portion
M c g	M. ceratoglossus
M c h	M. ceratohyoideus
M cr h	M. cricohyoideus
M d t	M. dermotemporalis
M g g	M. genioglossus
M hg a	M. hypoglossus anterior
M hg o	M. hypoglossus obliquus
M m h	M. mylohoideus
M s h	M. serpihyoideus
M st h	M. stylohyoideus
M tr h	M. tracheohyoideus
M tr l	M. tracheolateralis

DESCRIPTION

Skull

The skull of *Atrichornis* (Figs 1 and 2) has few features distinctly different from those usually present in small, insectivorous passerine birds. The brain and orbits are large, and dominate the total structure of the skull. The brain case of this specimen is fully ossified. Jaws are relatively short and straight with a large external nares and no ossification within the nasal cavity. The dorsal edge of the upper jaw rises gradually to a distinctive hump over the posterior end of the external nares, then drops off rapidly to the nasal-frontal hinge.The brain case is bulbous with a slightly projecting occipital region and an indistinct temporal fossa. The postorbital process is small and the zygomatic process almost nonexistent. Quadrates have distinct medial and lateral condyles and a moderate orbital process that terminates in a point. The ptergyoids are stout with well developed anterior feet embracing the basisphenoid rostrum. Palatines are straight and parallel with short transpalatine processes and strong prepalatine bars running forward to the upper jaw. A long slit separates the two halves of the bony palate with articulates with the basisphenoid rostrum only at the palatine-pterygoid junction. This slit extends to the anterior half of the vomer which has a narrow anterior plate and almost straight anterior edge. The maxillopalatines have moderately expanded medial plates.

The most unusual feature of the skull is the large, free lacrymal (or prefrontal) which extends from the frontal to the jugal bar (Fig. 1B). The dorsal head of this bone is small, and contacts the frontal along a narrow rim. A large gap separates the dorsal half of the lacrymal from ectethmoid plate, but the ventral halves of these two bones are in broad contact. The lacrymal does not fuse with any of the bones with which it articulates.

The mandible is straight with a narrow ramus and a moderate mandibular fossa. A distinct groove forms the articular surface for the medial condyle. Both the retroarticular process and the internal process of the mandible are short.

Jaw Ligaments

The four major avian jaw ligaments — the postorbital, the internal jugomandibular, the external jugomandibular and the occipitomandibular — are all present and well developed with the external jugomandibular being slighter weaker than the other. These ligaments have the normal passerine attachments and configurations (Fig. 3B; the occipitomandibular ligaments is not shown).

Salivary Glands

A special search was not made for the salivary glands so only the largest were noted. The G. angularis oris (Fig. 3B) lies medial and ventral to the jugal bar, ending just anteriorly to the postorbital ligament. The G. maxillaris (Fig. 6) lies along the choanal slit, medial to the M. pterygoideus, and covers the shelf of the palatine bone. The G. mandibularis (probably a combination of the mandibular and sublingual glands, Fig. 6) lies along the lateral edge of the M. pterygoideus, covering the lateroventral surface of the muscle. The ducts of these glands were not traced.

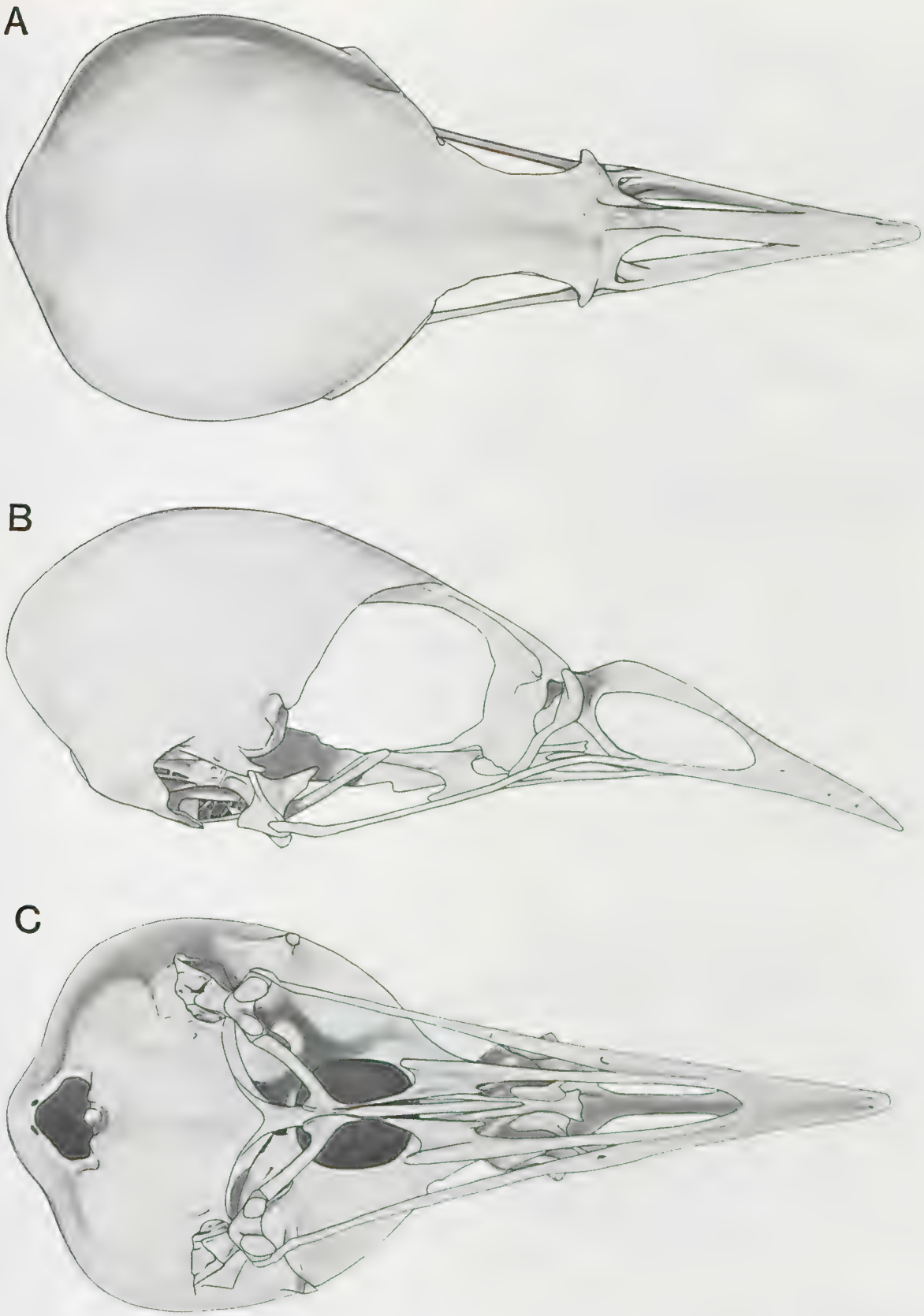

Fig. 1. Skull of *Atrichornis clamosus* seen in dorsal (A), lateral (B) and ventral (C) views. Note the large unfused lacrymal (l) articulating dorsally with the frontal.

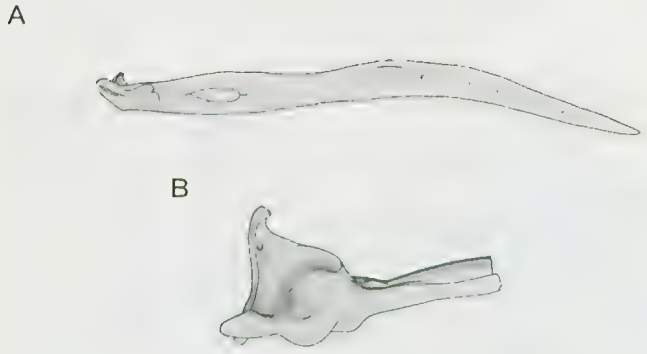

Fig. 2. Mandible of *Atrichornis clamosus* seen in lateral (A) and enlarged dorsal (B) views.

Jaw Muscles

The jaw muscles of *Atrichornis* (Figs 3, 4, 5, 6, 7 and 8) do not show any special features, being reasonably typical for an insect-eating passerine bird. Each muscle will be described individually but without special reference to the figures. See Bock (ms.) for discussion of the functions of these muscles.

M. depressor mandiulae (M d m). Origin is from the lateroposterior surface of the brain case and the lateral edge of the occipital plate. Insertion is on the posterior end of the mandibular ramus, the short retroarticular process and the posterior surface of the internal process of the mandible. The muscle is almost purely parallel-fibred with a fleshy origin and insertion.

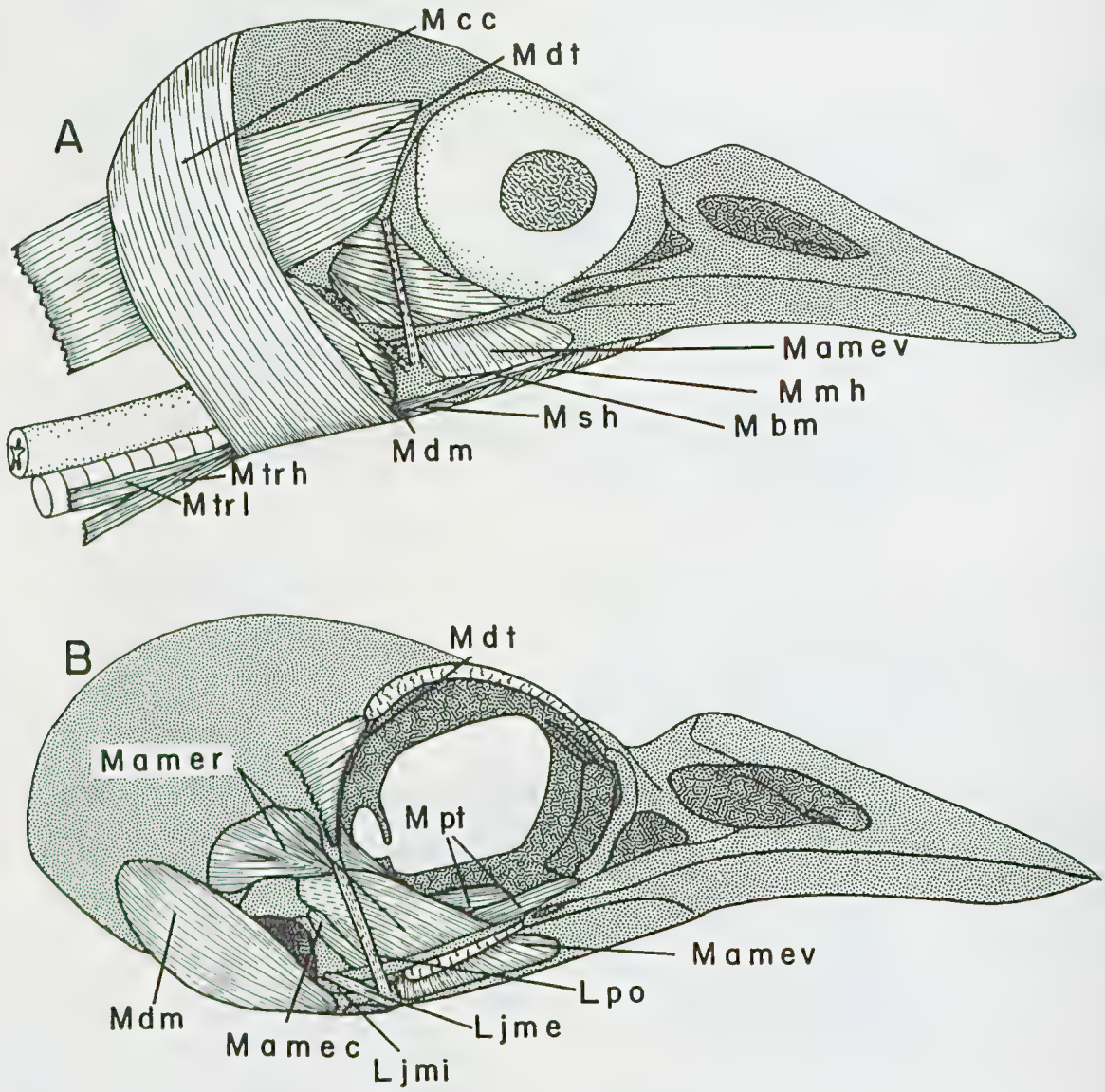

Fig. 3. Jaw and tongue musculature of *Arichornis clamosus* with (A) and without (B) the superficial M. cucullaris caput portion (M c c), M. dermotemporalis (M d t) and eye. See Methods section for abbreviations used in this and following figures.

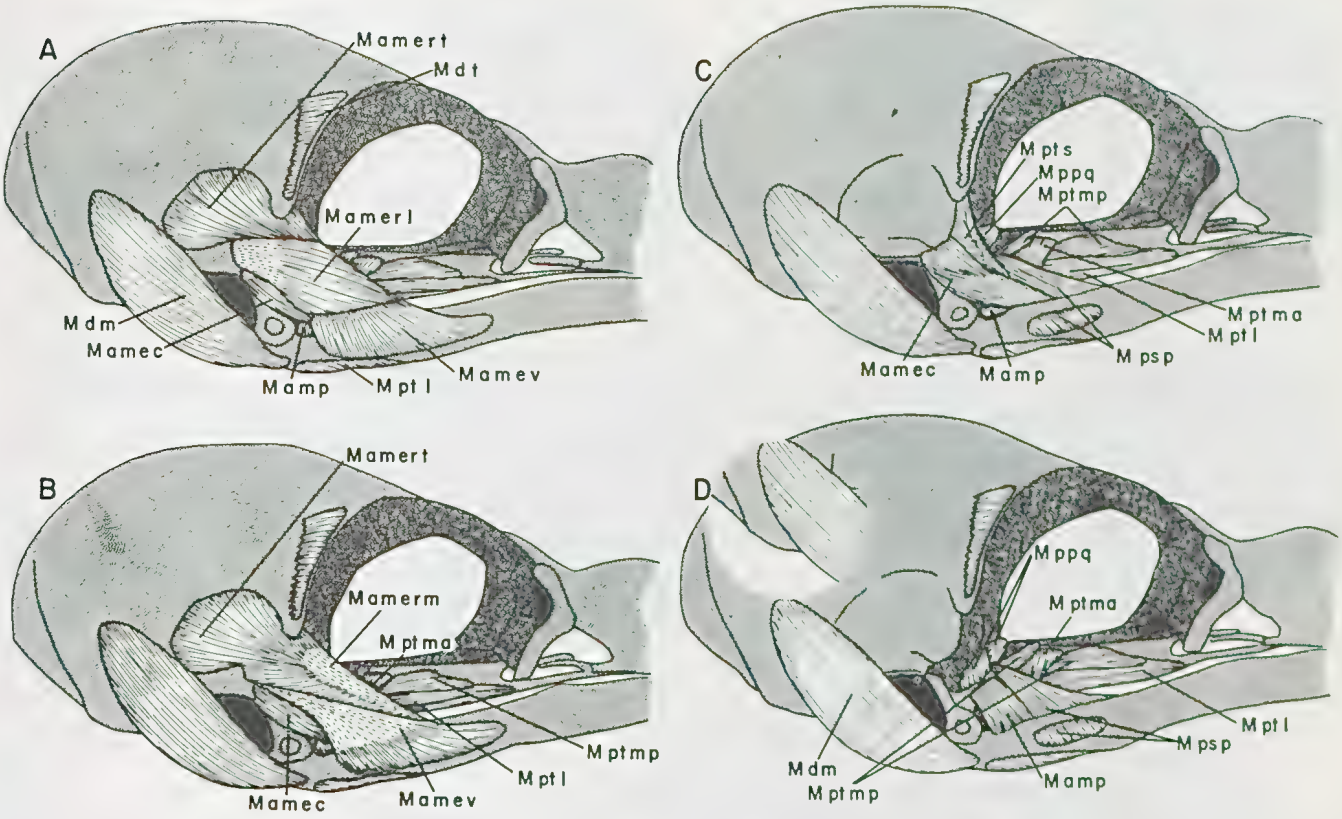

Fig. 4. Jaw muscles of *Atrichornis clamosus* seen in lateral view in successively deeper layers (A–D).

Longest fibres are 10 mm long with the shortest fibres (the medioventral portion) being only 3 mm long; most fibres are 6–7 mm long. The muscle is 3 mm wide, measured aong the lateral surface, and about 1.5 mm thick, given a fibre (= physiological) cross-sectional area (CSA = total cross-sectional area of all fibres) of about 4.5 mm². The occipitomandibular ligament lies buried in the medial part of the muscle.

M. adductor mandibulae externus. This is the largest and most complex component of the dorsal adductors; it is subdivided into three parts which merge somewhat into one another deep within the muscle. Each of the subdivisions will be described separately.

M. ADDUCTOR MANDIBULAE EXTERNUS ROSTRALIS (M a m e r). This portion of the adductor mandibulae externus has three reasonably distinct divisions — the temporalis (M a m e r t), the medialis (M a m e r m) and the lateralis (M a m e r l) — which will be described separately; however it must be stressed that these divisions merge into one another even more than do the parts of the adductor mandibulae externus. The temporalis originates from the temporal fossa and from the area medial to the postorbital process where it merges without a break into the medialis. Its fibres are arranged from fan-shaped to slightly bipinnately. Fibre length varies from short anterior fibres (2 mm) to longest posterior ones with an average of about 3 mm. The muscle width (surface measurement) is approximately 4 mm and thickness about 2 mm with a fibre CSA of 8 mm². The lateralis is the most superficial portion of the muscle and originates from the surface of a broad aponeurosis arising from the skull between the temporal fossa and the otic head of the quadrate. This position has a flat spindle shape with the fibres arranged unipinnately. Fibres are 3–4 mm long with the muscle being 4 mm wide and 0.75 mm thick for a fibre CSA of 3 mm². The medialis is the deepest part of the muscle and can only be seen in oblique view or when the superficial parts are dissected away. It arises from the lateral edge of the posterior wall of the orbit (lateral to the mandibular ramus of the trigeminal nerve), from the dorsal edge and medial surface of the aponeurosis of origin of the M a m e lateralis and from a broad aponeurosis forming the medial surface of the muscle; the last aponeurosis arises from the brain case just medial to the quadrate articulation. The muscle is bipinnate with a deep central tendon of insertion. Fibres are 3–4 mm long with the fibre CSA being 20 mm² (5 mm × 4 mm), making the medialis the largest segment of the rostralis. All three parts insert via a common tendon of insertion that attaches to the dorsal edge of the mandibular ramus at the anterior point of the muscle. The tendon lies deep within the muscle with fibres of the lateralis attaching to its lateral side, of the medialis to its medial and ventral surfaces, and of the temporalis to its free, posterior end.

M. ADDUCTOR MANDIBULAE EXTERNUS VENTRALIS (M a m e v). Origin is from the medial surface and the ventral edge of a broad aponeurosis arising from the tip of the short zygomatic process. Insertion is fleshy

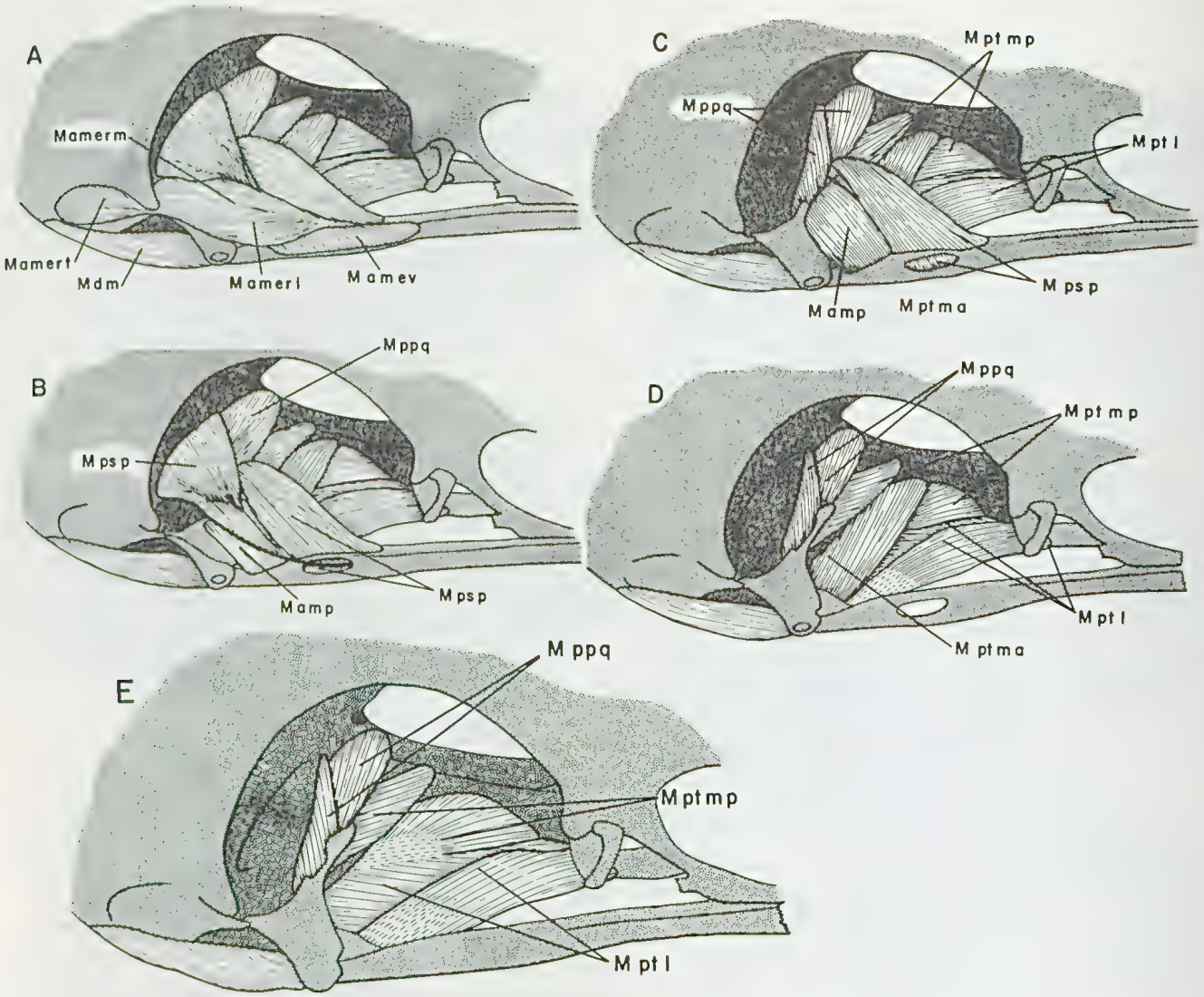

Fig. 5. Jaw muscles of *Atrichornis clamosus* viewed obliquely through the orbit in successively deeper layers (A–E).

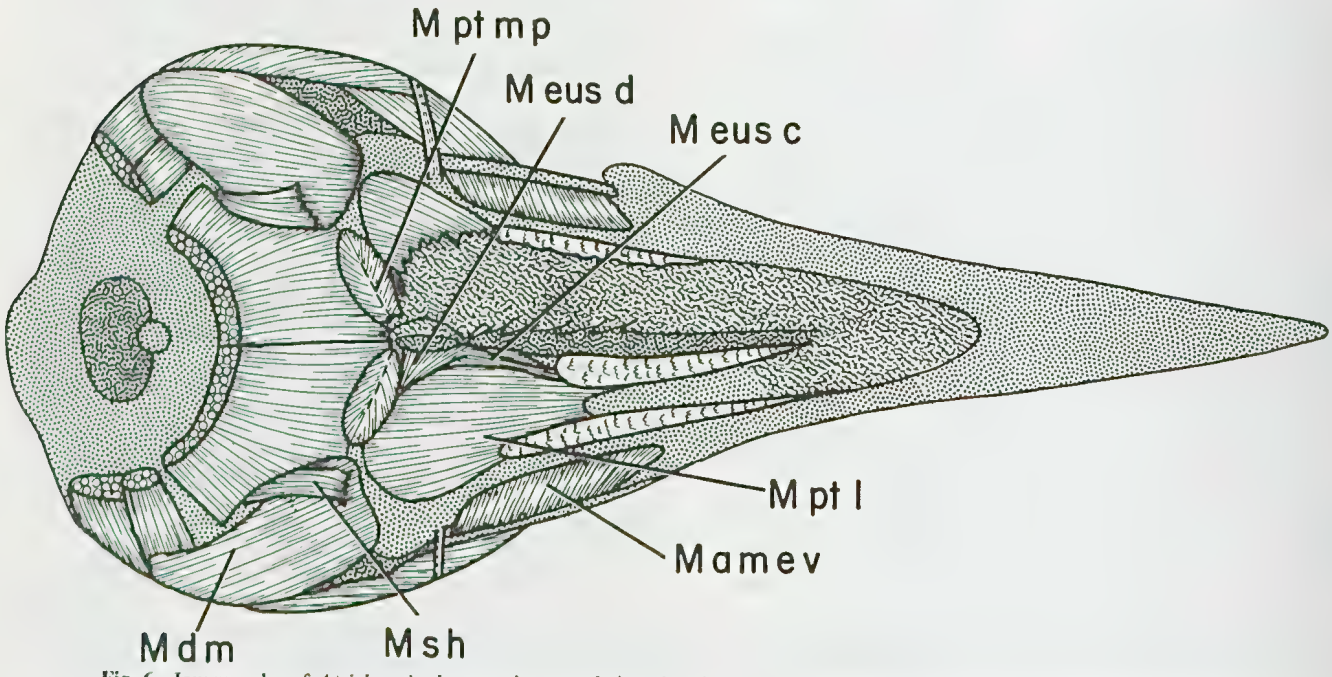

Fig. 6. Jaw muscles of *Atrichornis clamosus* in ventral view showing a general overview and the position of the major glands.

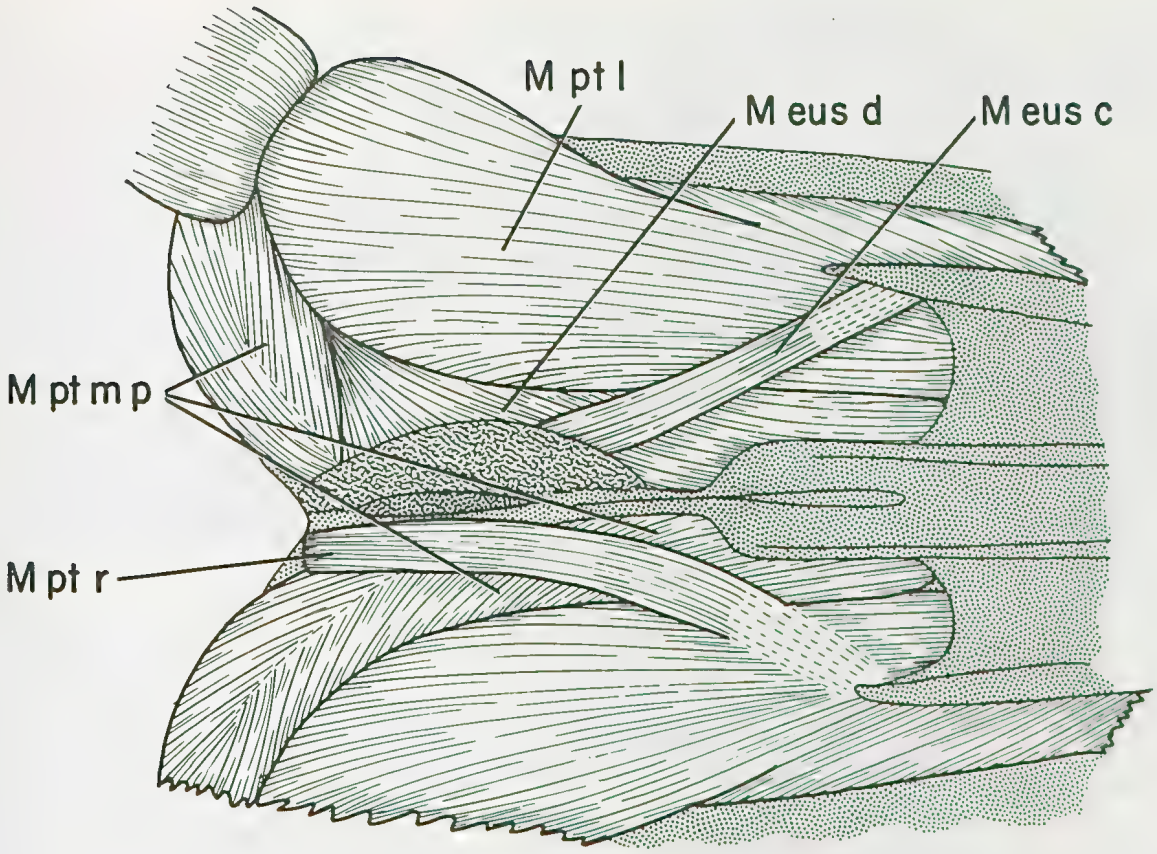

Fig. 7. Jaw muscles of *Atrichornis clamosus* in ventral view showing details of the muscles to the infundibulum and of the neighbouring position of the M. pterygoideus.

over a broad area of the lateral surface of the ramus around the mandibular fossa extending from the insertion of the M a m posterior to a point well anterior of the insertion of the M a m e rostralis. The ventralis is an unipinnate, fan-shaped muscle. Fibres vary from 2 mm (posterior) to 4 mm (anterior) long with a fibre CSA of 10 mm² (5mm × 2mm). Fibres in the medio-dorsal part of this muscle merge with those of the M a m e rostralis, especially the medialis portion.

M. ADDUCTOR MANDIBULAE EXTERNUS CAUDALIS (M a m e c). Origin is from the brain case ventral and medial to the zygomatic process, from the posterior wall of the orbit medial to the quadrate articulation and from the dorsal end of the otic process of the quadrate; some fibres arise from a short aponeurosis on the medial surface of the muscle. Insertion is on the dorsal edge of the ramus, dorsal to the posterior end of the mandibular fossa, partly fleshy but mainly via a superficial aponeurosis covering the anteromedial surface of the muscle. The dorsomedial fibres from the braincase are arranged unipinnately, and attach to the anterior aponeurosis while the ventroposterior fibres from the quadrate attach partly fleshy, but mainly unipinnately, on the aponeurosis of insertion. Fibre length is 2–3 mm with the shorter fibres arising from the quadrate; the fibre CSA is approximately 8 mm² (4 mm × 2 mm). The caudalis lies posterior and deep to the rest of the M a m externus, and is relatively short and thick compared to the other parts of the externus.

M. pseudotemporalis superficialis (M ps s). Originates from the posterior wall of the orbit extending medially from the origin of the M a m externus almost to the foramen for the optic nerve. Insertion is by a single tendon to the medial surface of the mandibular ramus just anterior to the quadrate articulation. The m ps superficialis is complexly pinnate with a faint indication of three parts (trifed) with a lateral and two internal tendons of origin. The superficial fibres of the muscle appear to be arranged in a parallel fashion, but the true pinnate configuration of the muscle is revealed by dissection. The muscle is 5 mm wide at its base and 10 mm long. Most fibres are 2–3 mm long with a fibre CSA of at least 20 mm² and possibly 25 mm². The inserting end of the M ps superficialis separates the M ps profundus and the M a m posterior.

M. pseudotemporalis profundus (M ps p). Origin is from the distal half of the orbital process of the quadrate; the entire origin is fleshy. Insertion is fleshy and mainly on the medial surface of the ramus about the mandibular fossa, but also along the dorsal edge of the ramus between the insertions of the M a m e rostralis and the M a m e caudalis. The M ps profundus is parallel-fibred and fan-shaped. Fibres are 6 mm, or more, long with a fibre CSA of 6 mm² (2 mm × 3 mm). The separation of the M ps profundus from the M a m posterior is quite arbitrary, being determined

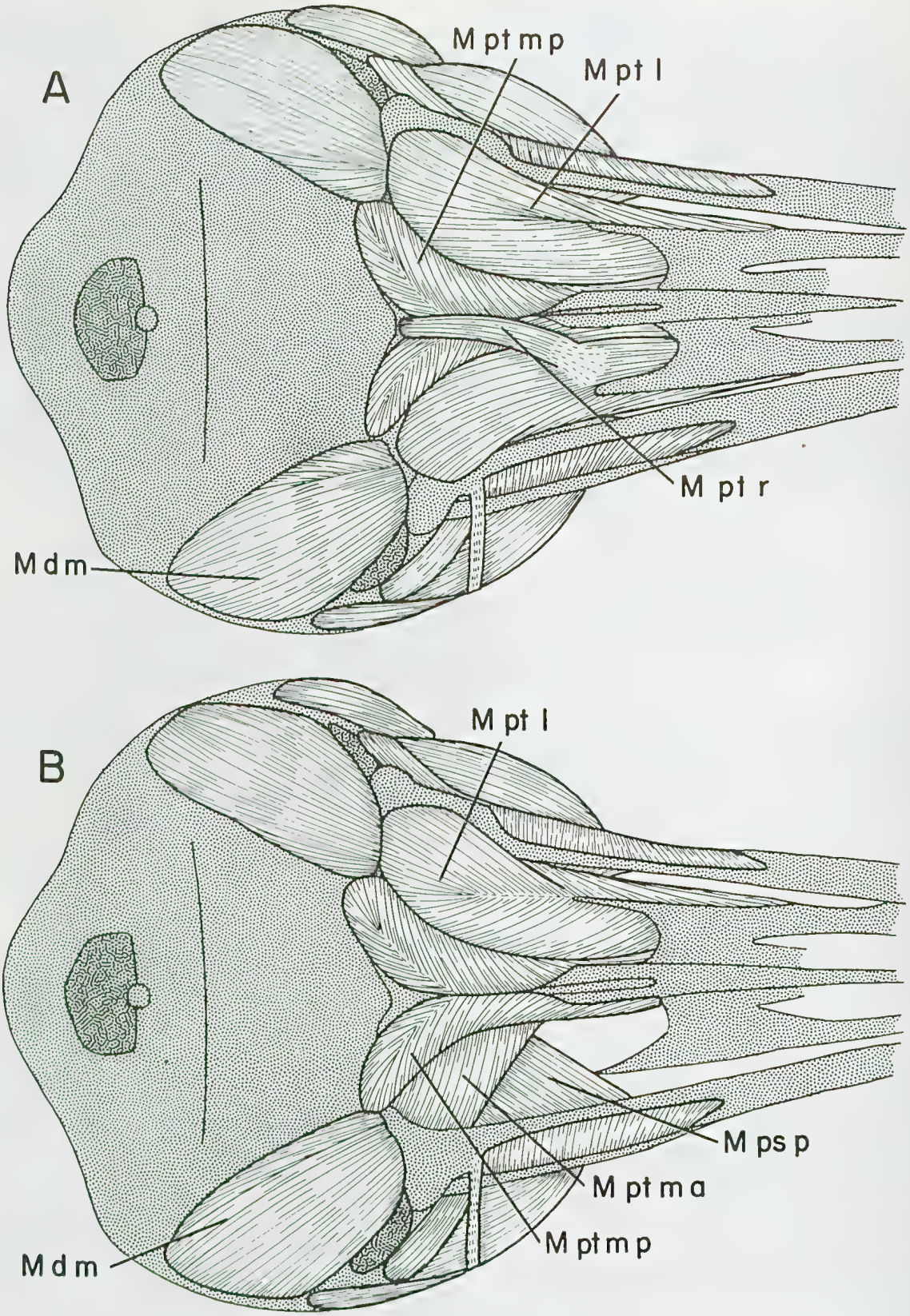

Fig. 8. Jaw muscles of *Atrichornis clamosus* in ventral view showing the M. pterygoideus in successively deeper layers (A–B).

mainly by the position of the pterygoid branch of the trigmeninal nerve. These two muscles are best merged into a single muscle, the M. quadromandibularis, which cannot even be subdivided into two parts in the passerine birds (Bock, ms.).

M. adductor mandibulae posterior (M a m p). Origin is from the basal half of the orbital process of the quadrate and ajoining part of the quadrate body. Insertion is on the lateral surface and dorsal edge of the mandibular ramus from the quadrate articulation to the insertion of the M ps profundus, and on the broad shelf forming the anterior edge of the quadrate articulation of the mandible; the insertion of the M ps superficialis separates those of the M a m posterior and of the M ps profundus. It is a parallel-fibred muscle with fibres 2-3 mm long and a fibre CSA of 4 mm^2 (2 mm × 2 mm). The M a m posterior is a rather large muscle which cannot be seen until the M. adductor mandibulr externus and the M. pseudotemporalis superficialis are removed.

M. protractor pterygoidii et quadrati (m p p q). Originates from the ventral part of the posterior wall of the orbit, from a point just medial to the quadrate articulation to a point anterior and ventral to the orbital foramen. Part of its origin is ventral to the origin of the M ps superficialis. Insertion is on the posterodorsal surface of the pterygoid, close to its quadrate articulation, and on the posterior surface of the orbital process of the quadrate and adjoining body of the quadrate. A few fibres attach to the anterior surface of the orbital process. The muscle appears to have two distinct parts but this results only from the arrangement of the superficial fibres; the deeper fibres merge together without a break. The muscle is mainly parallel-fibred but some of the fibres attaching to the pterygoid are unipinnate. Fibre length ranges from 4 mm (longest anteromedial) to 2 mm (shortest lateroposterior). The fibre CSA is about 8 mm^2 (5 mm wide × 1–2 mm thick).

M. pterygoideus. This large ventral adductor of the jaws is comprised of several parts which are reasonably distinct from one another; they will be described separately.

M. PTERYGOIDEUS INFUNDIBULARIS ANTERIOR (M pt i a) and M. PTERYGOIDEUS INFUNDIBULARIS POSTERIOR (M pt i p). These two small superficial slips on the ventral surface of the muscle are derived from, and are incompletely separated from, the adjoining parts of the M. pterygoideus. These muscles were first described by Richards & Bock (1973:66–67, based on the unpublished Ph.D. thesis of Richards) and described under the name "fan-like part" of the M pt medialis which is the M pt i posterior; the M pt i anterior was not described. A full description of these muscles is provided by Bock (ms.). The strap-like M pt i anterior arises from the medial surface of the transpalatine process, along with the M pt retractor, and inserts on the lateroanterior edge of the infundibular slit. It serves to close the opening of the infundibular slit by pulling the two lips forwards and thereby straightening them against each other. The fan-shaped M pt i posterior originates along most of the lateral edge of the infundibular lip and inserts via a thin tendon on the tip of the internal process of the mandible, along with the large tendons of the M pt medialis posterior. It serves to open the infundibular slit by pulling the two lips laterally and away from one another. Both muscles are very thin slips and are easily damaged or destroyed when removing the mucosa lining the roof of the mouth prior to the dissection of the M. pterygoideus.

M. PTERYGOIDEUS LATERALIS (M pt l). This muscle was frequently divided into a ventral and dorsal portion but recent study (Bock, ms) suggests that this is an artificial division along the plane of an aponeurosis of origin. Origin is from the dorsal surface of the transpalatine process and the palatine shelf, and from a tendon arising from the tip of the transpalatine process. Two aponeuroses of insertion exist — one on the dorsal surface of the muscle that attaches to the corner between the ramus and internal process of the mandible and one on the medial surface (in common with the M pt m posterior) that attaches to the tip of the internal process of the mandible. Fibres spread out from the origin of the muscle to these several areas of insertion. Most fibres are about 3 mm long with a total fibre CSA of 24–28 mm^2 (4 mm × 6–7 mm). The M pt lateralis merges with the M pt m posterior along its medial border.

M. PTERYGOIDEUS MEDIALIS POSTERIOR (M pt m p). Earlier studies had divided the medial part of the M. pterygoideus into a ventral and a dorsal portion, and further subdivided the dorsal portion into anterior and posterior divisions. Recent analysis (Bock, ms.) suggested that the division of the medialis into ventral and dorsal parts is artificial and that the primary division is whether the portion arises from the anterior or the posterior surface of the pterygoid. The posterior part usually extends ventral to the pterygoid to originate from a major part of the mediopalatine process and even from the shelf of the palatine. Thus, much of the posterior part of the M pt m posterior may be anterior to the M pt m anterior. The M pt m posterior originates from the lateral surface of the mediopalatine process, bipinnately from a tendon arising from the posterior end of the mediopalatine process and from the posterior surface of the pterygoid. It inserts on an aponeurosis lying along the lateral surface of the muscle (in common with the M pt lateralis), on an aponeurosis along the posterior surface of the muscle and, by a few fibres, directly on the tip of the internal process of the mandible; the inserting aponeuroses attach to the tip of the internal process of the mandible. It is mainly unipinnate, but the posterior third is bipinnate. Fibres are 1–2 mm long (average about 1.5 mm) with a fibre CSA of about 10 mm^2 (1 mm × 10 mm). The M pt m posterior lies mainly ventral to the pterygoid except for the portion that takes origin from this bone.

M. PTERYGOIDEUS MEDIALIS ANTERIOR (M pt m a). Origin is from the anterior surface of the pterygoid and from a small area on the lateral surface of the

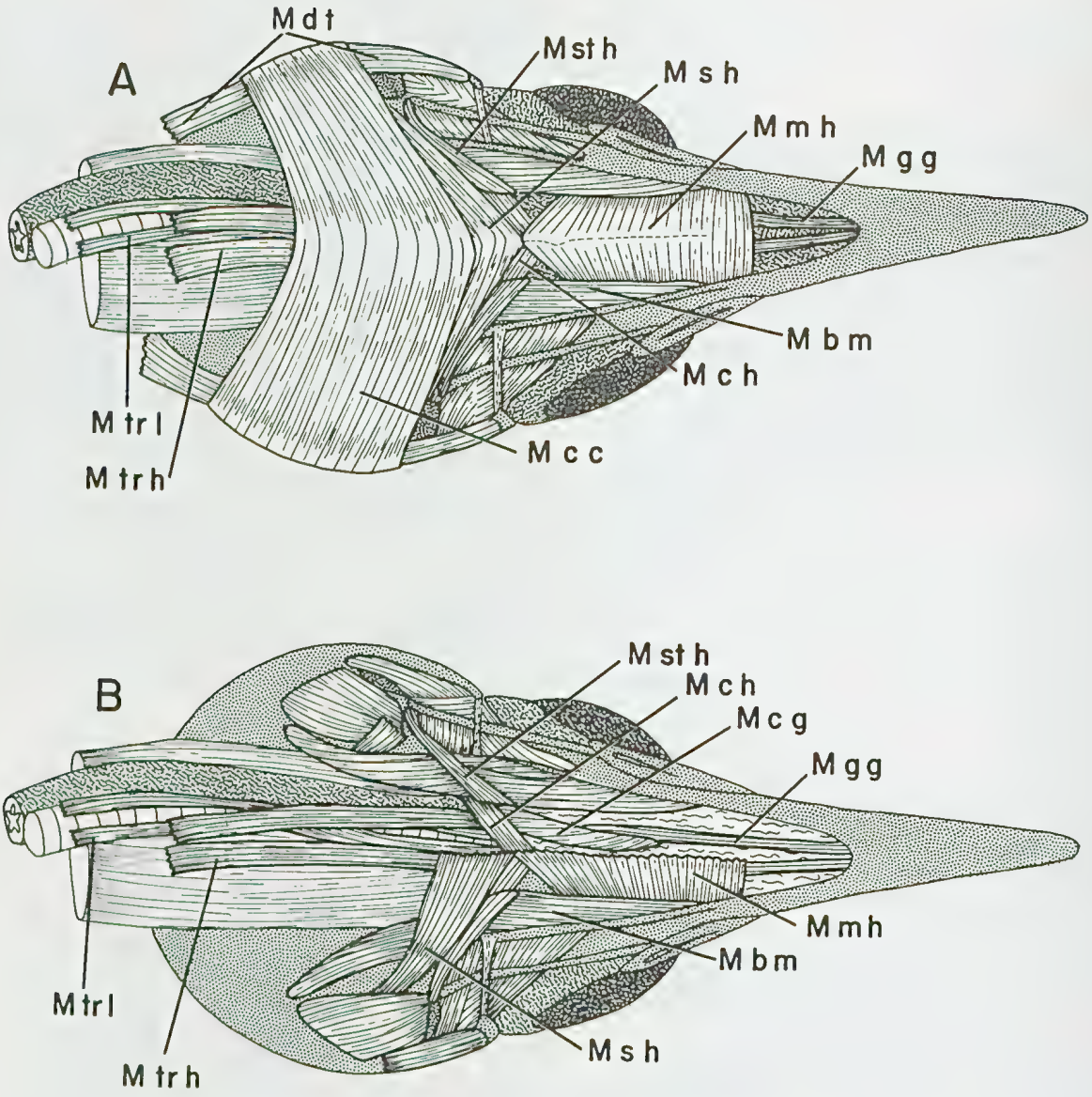

Fig. 9. Tongue muscles of *Atrichornis clamosus* in ventral view with (A) and without (B) the superficial M. cucullaris and M. dermotemporalis. The M. mylohyoideus and M. serpihyoideus have been removed from the right side in Figure B. In this and following drawings, the muscles and other structures of the neck have been extrapolated posterior from the level of the occipital condyle (apprximately at the posterior border of the M. cucullaris) where the head was severed from the neck.

mediopalatine process just anterior to the pterygoid articulation. Insertion is at the corner of the ramus and internal process of the mandible medial to that of the M a m posterior; insertion is mainly fleshy. It is mostly parallel-fibred, but a few fibres may be unipinnate. Fibres are 5–6 mm long with a fibre CSA of 2 mm² (4 mm × 0.5 mm).

M. PTERYGOIDEUS RETRACTOR (M pt r). Origin is from the transpalatine process and from the superficial ventral aponeurosis of the M pt lateralis. Insertion is on the basitemporal plate just lateral to the midline. The M pt retractor is thin, parallel-fibred and strap-like with fibres 5–6 mm long and a fibre CSA of about 0.20 mm² (0.88 mm wide × 0.25 mm thick).

Tongue

The tongue (Fig. 10A) is slightly concave dorsally (Fig. 10C) with its anterior tip divided into two by a short medial cleft. Each of the two tips bears a number of short laciniae giving the tongue tip a frilled appearance. The extent of this frilling in *Atrichornis* is no greater than that seen in many insectivorous birds. It does not resemble in any special way the tongue of the Meliphagidae.

Tongue Skeleton

The bones of the hyoid in *Atrichornis* are typical for passerine birds with the exception of the basihyale. This

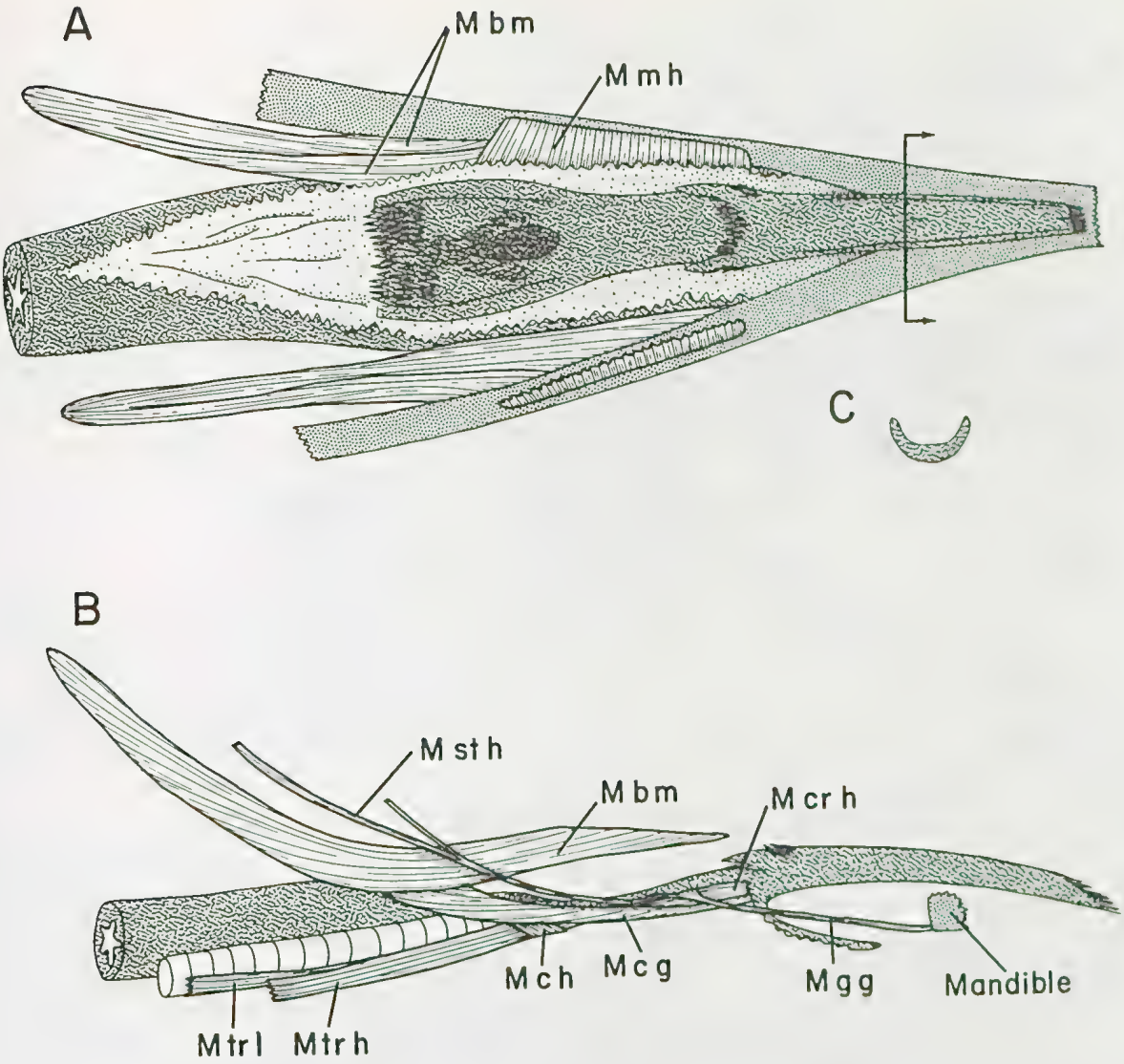

Fig. 10. Tongue and tongue musculature of *Atrichornis clamosus* in dorsal (A) and lateral (B) views, and cross section (C) of the tongue at the indicated level.

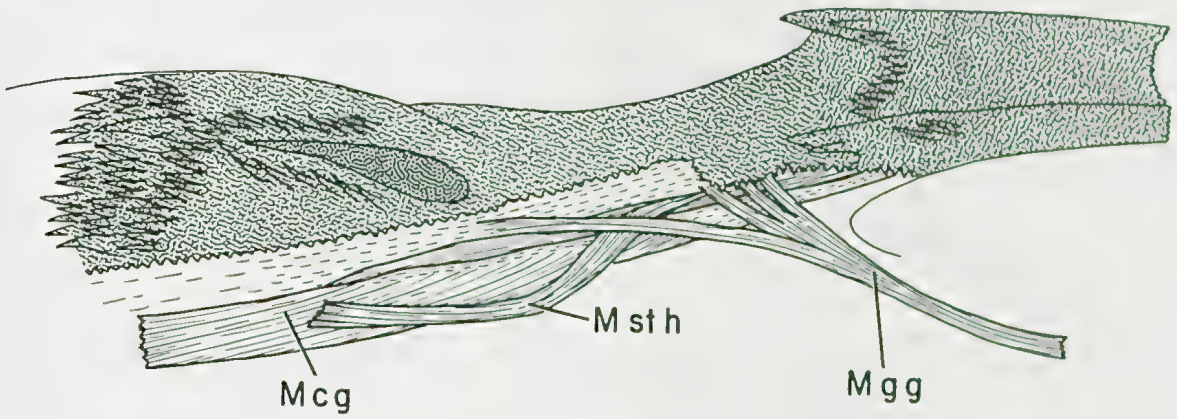

Fig. 11. Tongue of *Atrichornis clamosus* in dorsolateral view to show details of the insertion of the M. genioglossus into the mucosa between the tongue and the larynx.

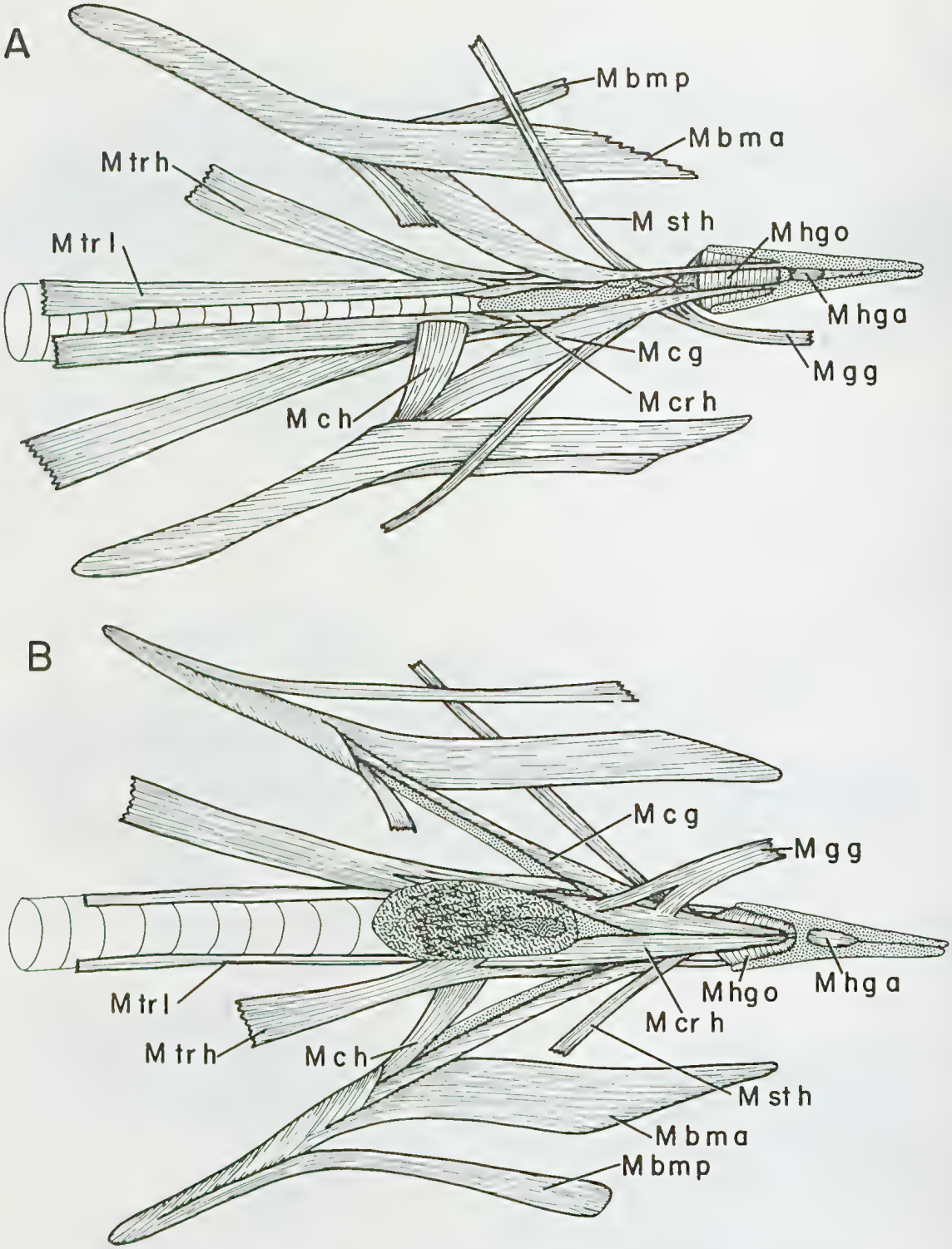

Fig. 12. Tongue muscles of *Atrichornis clamosus* in ventral (A) and dorsal (B) views. The M. mylohyoideus and M. serphihyoideus have been removed, the tongue and trachea dissected from the floor of the mouth and the structures spread out from the midline to show the individual muscles in greater detail.

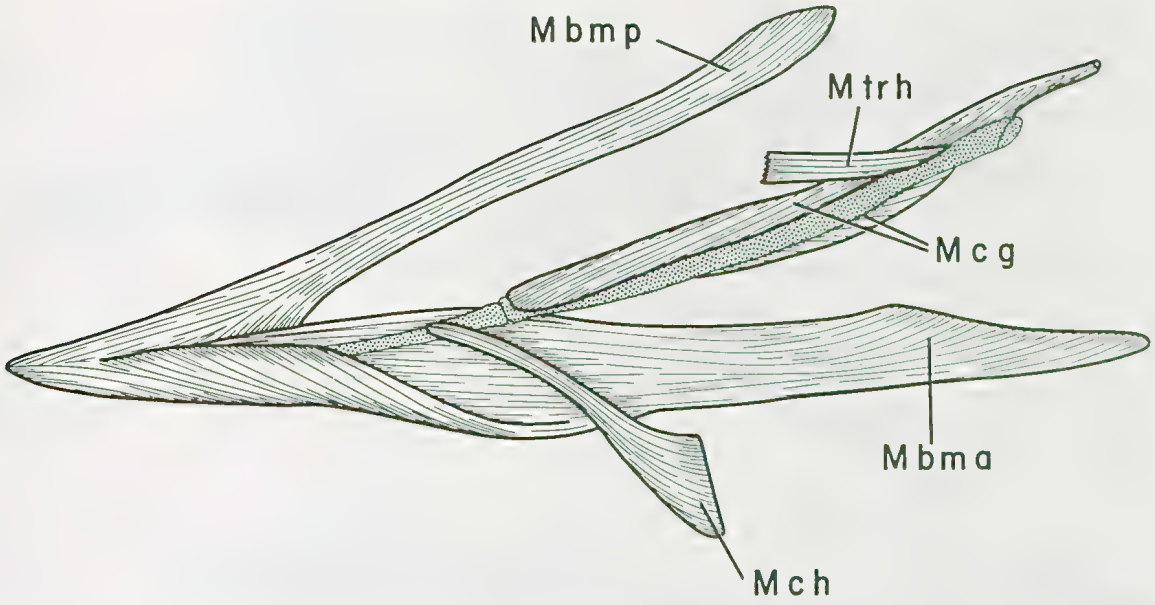

Fig. 13. Tongue muscles of *Atrichornis clamosus* in dorsal view to show the details of the muscles attaching to the hyoid horn; the muscles have been dissected and spread out for greater detail.

bone is slightly flattened laterally and has a distinct, sharp, ventral keel at its midpoint (Fig. 15).

Tongue Muscles

Atrichornis possesses all of the tongue muscles known for other passerine birds (Figs 3, 9, 10, 11, 12, 13, 14, 15 and 16). Two other muscles — the M. cucullaris and the M. dermotemporalis — will be described here because their dissection was done with that of the tongue muscles. The head of the *Atrichornis* specimen was severed from the neck before I received it. The cut was made at the occipital condyle at a level near the posterior edge of the M. cucullaris caput portion; hence it was not possible to trace any of the muscles into the neck. Most likely, the noncranial attachment of these muscles do not differ from those seen in other passerine birds. For purposes of drawing, the structures in the neck were extrapolated back for a short distance. Each muscle will be described individually but without special reference to the figures. See Bock (ms.) for a discussion of the functions of these muscles.

M. dermotemporalis (M dt). Origin is from the lateral surface of the brain case just behind the orbital rim (Fig. 3). The muscle runs posteriorly down the neck. It is covered by the M. cucullaris caput portion. The M. dermotemporalis is a parallel-fibred strap-like muscle with very long fibres. The fibre CSA is 2 mm^2 (4 mm wide × 0.5 mm thick).

M. cucullaris caput portion (M c c). Origin is from the dermis near the middorsal line of the posterior end of the brain case (Fig. 3). Insertion is on the contralateral muscle along the ventral midline of the head; actually, the fibres run continuously from origin to origin. The M. cucullaris is the most superficial muscle of the head and difficult to separate from the overlying skin. It is about 8 mm wide and very thin, about 0.1–0.2 mm thick; giving a fibre CSA of about 1 mm^2. Fibres on each half of the muscles are about 35 mm long for a total length of 70 mm.

M. mylohyoideus (M m h). Origin is from the medial surface of the mandibular ramus just below its dorsal edge. Insertion is on a midventral raphe with the contralateral muscle. The muscle is 10 mm wide, measured at the midventral line, and is 0.1-0.2 mm thick for a fibre CSA of 1–1.5 mm^2. Fibre length (for each muscle) varies from 3 mm for the short anterior fibres to 6 mm for the longest posterior fibres.

M. serpihyoideus (M s h). Origin is from the lateral edge of the basitemporal plate, medial to the origin of the M d mandibulae. Insertion is on the contralateral muscle at the ventral midline with the anterior end of the muscle attaching to the posterior end of the M. mylohyoideus. Fibres are 10 mm long with a fibre CSA of 3.0–0.6 mm^2 (3 mm wide × 0.1–0.2 mm thick).

M. stylohyoideus (M st h). Half of the muscle originates from the basitemporal plate, along with the M. serphihyoideus, and half from the lateral edge of the mandibular ramus just anterior to the insertion of the M d mandibulae. It inserts on the ventral surface of the basihyale just anterior to the ceratobranchial articulation. Fibres are 15–18 mm long with a fibre CSA of 0.03 mm^2–0.05 mm^2 (0.3–0.5 mm × 0.1 mm). The M. stylohyoideus is a thin, narrow, strap-like muscle and is vestigal in *Atrichornis*.

M. branchiomandibularis (M b m). This muscle has two parts — an anterior and a posterior — but they can be described together. The M b m anterior originates from the medial surface of the mandibular ramus, ventral to the origin of the M. mylohyoideus. The

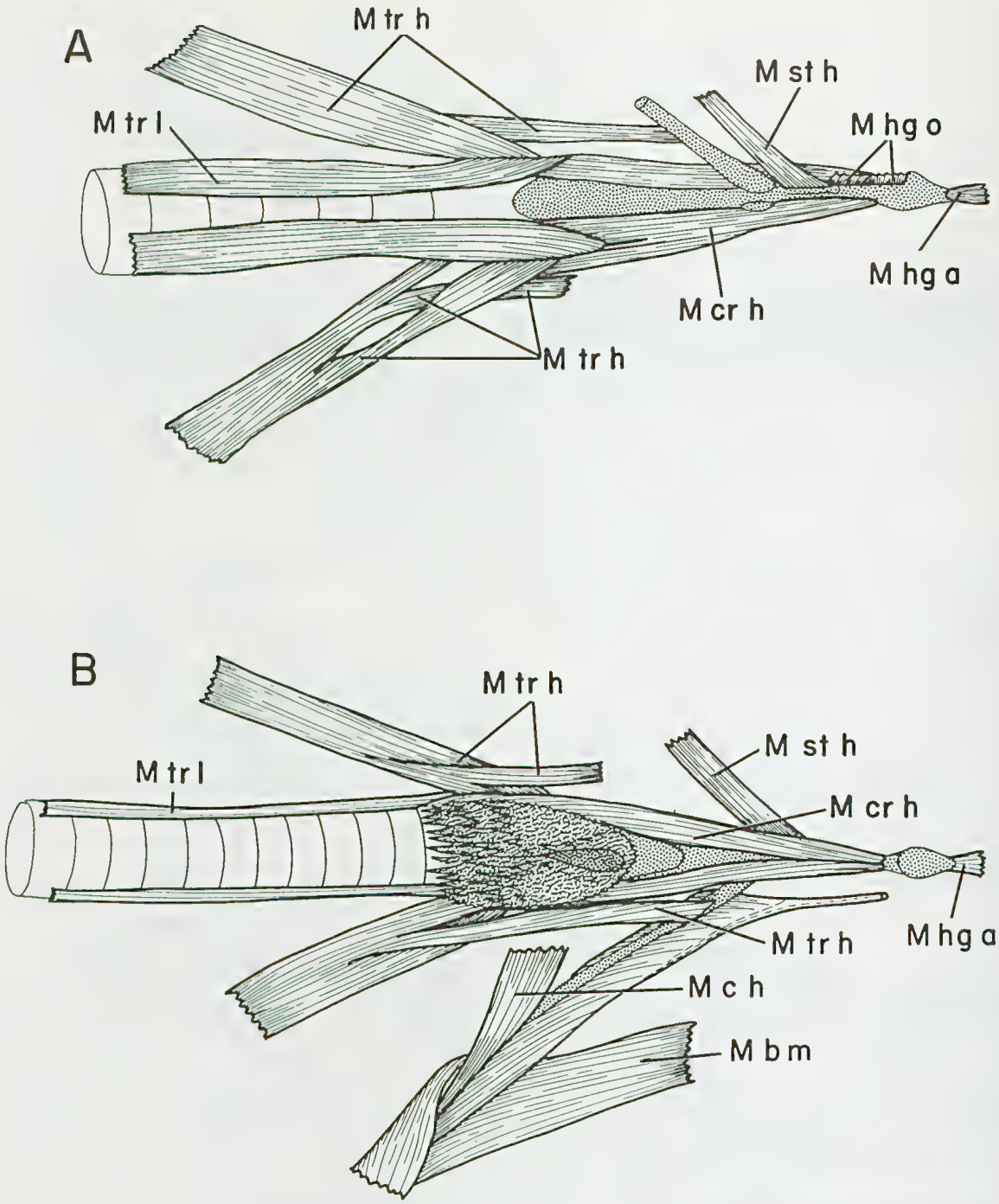

Fig. 14. Tongue muscles of *Atrichornis clamosus* in ventral view (A) and dorsal view (B) to show the details of the muscles attaching to the basihyale and the larynx. The paraglossalia and the left hyoid horn have been removed.

M b m posterior originates from the ventral edge of the mandible, ventral to the anterior half of the M a m e vetralis. Both parts merge and insert on the distal end of the epibranchiale. The M. branchiomandibularis is a parallel-fibred muscle which wraps about the hyoid horn to encase these bones completely. Fibres are 20–25 mm long with a fibre CSA of 1 mm^2 (2 mm × 0.5 mm) for the larger anterior part and 0.55 mm^2 (0.75 mm × 0.75 mm) for the smaller posterior portion.

M. ceratahyoideus (M ch). Origin is from the dorsolateral surface of the epibranchiale just above the ceratobranchial articulation. Insertion is with the contralateral muscle on the midventral line, dorsal to the posterior end of the M. mylohyoideus. The insertion of the M. ceratohyoideus is bound to that of the overlying M. mylohyoideus and M. serpihyoideus. The M. ceratohyoideus passes dorsal to the epibranchiale as it extends from its origin to insertion. It is a parallel-

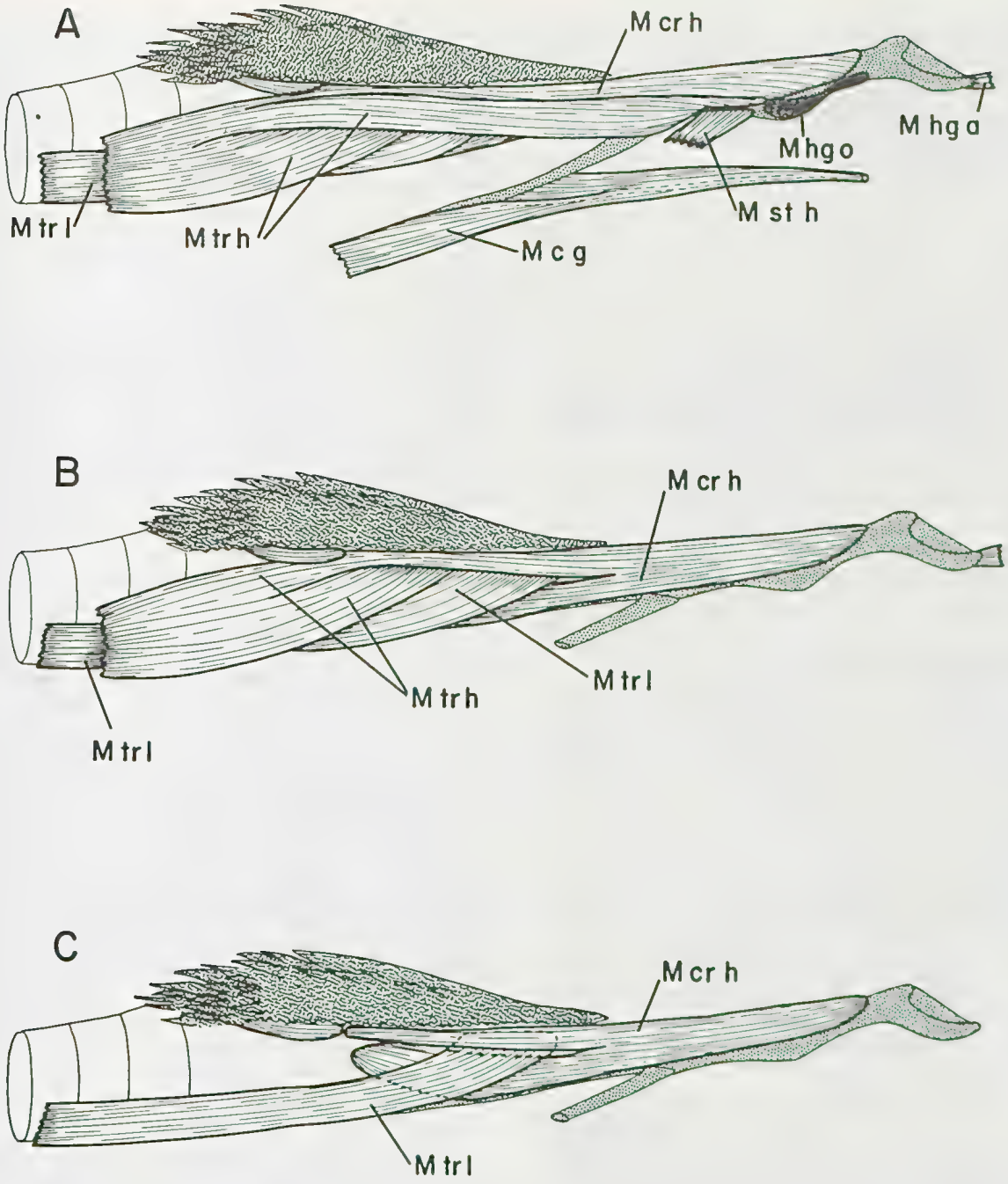

Fig. 15. Tongue muscles of *Atrichornis clamosus* in lateral view in successively deeper levels (A–C) to show the details of the muscles attaching to the basihyale and the larynx. The paraglossalia and most of the hyoid horn have been removed.

fibred, strap-like muscle (slightly fan-shaped) with fibres 7 mm long and a fibre CSA of 0.18–0.28 mm^2 (maximum, 0.3–0.4 mm × 0.6–0.7 mm). The muscle is 2 mm wide at its insertion.

M. genioglossus (M g g). Origin is from the posterior edge of the mandibular synthesis (Fig. 10B). Insertion is by several slips into the mucosa between the tongue and the glottis (Fig. 11), but not to the paraglossale. The M. genioglossus lies superficial to other tongue muscles at its insertion. Parallel fibres of this strap-like muscle are 10–12 mm long and have a fibre CSA of 0.06–0.08 mm^2 (0.3–0.4 mm × 0.2 mm).

M. ceratoglossus (M c g). Origin is along the whole length of the ceratobranchiale, mainly from the ventral surface but partly from the lateral surface. All fibres attach pinnately to a stout tendon lying on the ventrolateral edge of the muscle and attaching to the medioventral corner of the paraglossale just anterior to the basihyale articulation. The M c hyoideus is a unipinnate, two-joint muscle 16 mm long, 1.5 mm wide

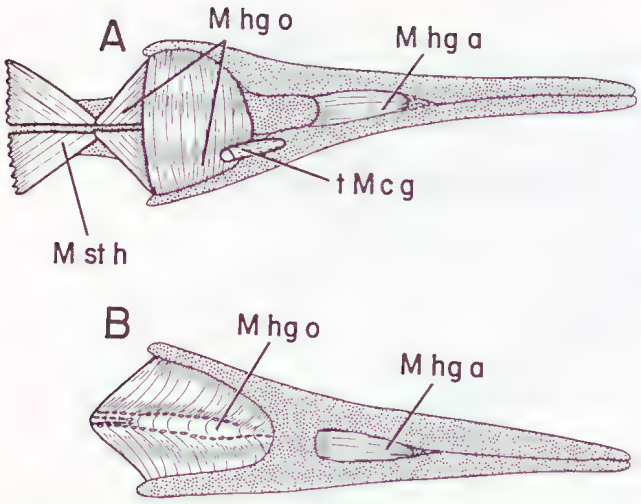

Fig. 16. Tongue muscles of *Atrichornis clamosus* in ventral (A) and dorsal (B) views to show the details of the muscles attaching to the paraglossalia.

and 0.8–1.0 mm thick. Fibres are 4–5 mm long and the fibre CSA is approximately 15 mm² (10 mm × 1.5 mm).

M. hypoglossus obliquus (M hg o). Origin is from the medioventral surface of the entire posterior process of the paraglossale. The ventral fibres pass ventral to the basihyale from origin to origin, while the deeper (dorsal) fibres insert on the basihyale; perhaps one-fourth of the M. hg obliquus inserts on the basihyale. The M hg obliquus has two indistinctly separable parts. Most fibres are parallel and lie transversely to the longitudinal axis of the tongue. A posterior portion has fibres lying sharply obliquely to the anterior fibres. Although this posterior part appears to be very distinct in ventral view (Fig. 16A), this distinction fades when one dissects through the muscle or examines the muscle in dorsal view (Fig. 16B). Fibre length is 3 mm (origin to origin) or 1–1.5 mm from origin to insertion on basihyale. The fibre CSA is 1–1.5 mm² (2 mm wide × 0.5–0.75 mm thick).

M. hypoglossus anterior (M hg a). Origin is from the ventral tendinous sheath that binds the two paraglossalia together. All fibres insert on the anterior tip of the basihyale between the two paraglossalia; no fibres insert on the paraglossale. The M hg anterior is a single medial muscle with no signs of a division into two muscles as in most passerine birds. All fibres are parallel to the longitudinal axis of the tongue. Fibres are 1.55 mm long with a fibre CSA of 0.15 mm² (0.55 mm wide × 0.03 mm thick).

M. cricohyoideus (M cr h). Origin is from the dorsolateral edge (small head) and from the ventrolateral surface (large head) of the cricoid (Fig. 15). The two heads of origin of the M cr hyoideus are separated by the insertion of part of the M tr hyoideus and the insertion of the M tr lateralis. The larger ventral head of the M cr hyoideus passes deep (medially) to the inserting end of the M tr lateralis. A few fibres from the dorsal edge of the M tr hyoideus merge into the dorsal head of the M cr hyoideus. The two heads of the muscle merge close to the anterior end of the cricoid and insert on the dorsal surface of the basihyale just off the middorsal line and just posterior to the paraglossale articulation. It is a parallel-fibred, strap-like muscle with fibres 19–20 mm long and a fibre CSA of about 1 mm² (1 mm × 1 mm). The M. cricohyoideus is the main retractor of the tongue in *Atrichornis* because of the vestigial nature of the M st hyoideus.

M. tracheohyoideus (M tr h). Origin was severed from head in this speicmen, but is presumably similar to that seen in other passerine birds, i.e., from the surface of the M. pectoralis or from the furcula. It inserts via three different slips. The largest slip, which comprises approximately the ventral three-fourths of the muscle, inserts on the ventrolateral surface of the cricoid, just posterior to the insertion of the M tr lateralis. The second slip, about one-fourth of the muscle, runs forward to insert on the lateral surface of the proximal end of the ceratobranchiale, with a few fibres running forward to insert on the basihyle. A small number of fibres from the dorsal edge of the muscle comprise the third slip and merge into the dorsal head of the M cr hyoideus. This strap-like, parallel-fibred muscle has very long fibres that extend from the furcula to the anterior end of the trachea, and has a fibre CSA of 0.5–1.0 mm² (2 mm wide × 0.3–0.5 mm thick).

M. tracheolateralis (M tr l). Origin was severed from head in this specimen, but presumably is from the syringeal aponeurosis as in *Menura* (see Ames, 1971). Insertion is on ventrolateral surface of the cricoid, approximately at the level of the anterior end of the glottis; it lies over the ventral head of the M cr hyoideus (Fig. 15C). This strap-like, parallel-fibred muscle has very long fibres (same approximate length as those of the M tr hyoideus) and has a fibre CSA of 0.6–1.00 mm² (2 mm wide × 0.3–0.5 mm thick).

DISCUSSION

Only limited comparisons could be made between *Atrichornis* and *Menura*, and no meaningful ones between *Atrichornis* and other passerine birds because of time restrictions; these studies have been planned and will be reported on in the future. A few conclusions can be presented now on the cranial osteology and on the tongue musculature.

Comparison of the skull of *Atrichornis* with that of *Menura* shows a number of similarities as well as differences; most are hard to evaluate. Most of the similarities could be as easily attributed to general passerine resemblance as to a reflection of close affinity of these genera. Many of the differences may be associated with the much larger size of *Menura* which has a skull about 3 times that of *Atrichornis* in linear measurements.

One feature that is shared by the two birds is the large, free lacrymal that articulates dorsally with the frontal, ventrally with the jugal and medially with the ectethmoid plate; it is not fused with any of these neighbouring bones. The morphology of the lacrymal does differ in these two genera, with the bone being smaller and with a much reduced dorsal head in *Atrichornis*. The large, free lacrymal of *Atrichornis* and *Menura* is very unusual for passerine birds; otherwise found only in the bowerbirds (Ptilonorhychidae; Stoner, 1937; Bock, 1963). Although the lacrymal of *Menura* is quite similar to that seen in the bowerbirds, as first pointed out by Stoner, the lacrymal of *Atrichornis* differs considerably from that of the bowerbirds. Moreover, aside from the lacrymal, the overall morphology of the skull of both *Atrichornis* and *Menura* differs markedly from that of the bowerbirds, compared to the range of variation of skull morphology seen in all passerine birds, in spite of the claim by Sibley (1974) that the skull of *Menura* is, overall, similar to that of the bowerbirds.

A reasonable functional-adaptive explanation for the large lacrymal in *Menura*, *Atrichornis* and the bowerbirds cannot be offered at present.

The morphology of the skull provides support, although not very strong, for the close relationship of *Atrichornis* to *Menura*. Granting the close similarity of the lacrymal in *Menura* and in the bowerbirds, the cranial osteology does not offer, at this time, any special support for the conclusion postulated by Sibley (1974, 1976; Sibley & Ahlquist, 1985, in press) that lyrebirds are close relatives of the bowerbirds and are part of the Australian 'corvine assemblage'.

The jaw muscles offer almost no information on the possible evolutionary history and on the affinities of *Atrichornis* at the current state of our knowledge; however, the tongue muscles exhibit several peculiar attributes and permit some comments on the status of *Atrichornis*. These conclusions depend upon a broad comparative study of the tongue musculature that I have made, but is mainly unpublished (Bock, ms.). They will not permit an assessment of the taxonomic position of *Atrichornis*, only an indication of the evolutionary change in its tongue morphology from that of other oscine birds. I will not give reasons supporting conclusions on the primitiveness versus advancedness of different configurations of the tongue musculature, or of possible reversals of change, largely because most of my conclusions are not based on really convincing arguments (see Bock, 1977 for a discussion of methods and Bock, ms. for a discussion of the diversity seen in passerine tongue muscles).

The M. genioglossus has two slips of insertion in most passerine birds, one to the psoterolateral surface of the paraglossale and one to the mucosa between the tongue and the glottis. The former insertion is lacking in a number of species, some with very different feeding habits as, for example, *Coccothraustes* and *Arachnothera*. I suspect that presence of the paraglossal insertion is primitive in passerine birds and that its loss is advanced, but cannot eliminate the possibility of reevolving the paraglossal insertion once it has been lost.

The M. stylohyoideus is the main retractor of the tongue in passerine birds, but has become vestigial in a few genera in the Meliphagidae with the M. cricohyoideus or a digastric M. stylohyoideus-serpihoideus becoming the main tongue retractor. These forms are nectarivorous with relatively long protrusion and retraction of the tongue. The vestigial M. stylohyoideus in *Atrichornis* is puzzling because this bird has a short tongue with no evidence of long protraction and retraction. The vestigial condition of this muscle would be advanced, but reversed evolutionary change would be easily possible so long as the muscle does not disappear completely.

In most passerine birds possessing a M. hypoglossus anterior, this muscle arises from the midventral connective tissue between the paraglossalia and inserts on the paraglossale, anterior to the attachment of the M. ceratoglossus. Insertion to this muscle to the anterior end of the basihyale is one of the several advanced states of the M hg anterior and is seen in *Dicaeum*, *Oedistoma* and *Promerops*. Usually, only part of the muscle inserts on the basihyale. Complete insertion of the M hg anterior on the basihyale in *Atrichornis* is advanced, but reversed evolution to an insertion on the paraglossale appears to be easily possible.

Generally, in passerine birds, the M. hypoglossus obliquus passes beneath the basihyale without inserting on this bone; the muscle forms a sling between the two paraglossalia. Insertion of the M hg obliquus on the basihyale is found in *Dicaeum*, *Passer*, *Coereba*, some emberizines, fringillids and drepanidids among others. (In most New World nine-primaried oscines, the M hg obliquus *does not* insert on the basihyale.) Insertion of the M hg obliquus on the basihyale appears to be advanced and I suspect that reversed evolutionary change to the sling-like structure is improbable because the inserting muscle appears to have all the functions and adaptive advantages of the sling-like arrangement. The partly inserting arrangement in *Atrichornis* would be advanced. The semidivision of this muscle is probably also advanced.

Typically, in passerine birds, the M. ceratohyoideus originates from the medial surface of the posterior end of the ceratobranchiale; this appears to be the primitive condition. In a few genera, e.g. *Corvus* and *Moho*, part or all of this muscle arises from the lateral surface of the ceratobranchiale. In a few, the origin of the muscle extends to the epibranchiale. The origin of the M c hyoideus from the dorsolateral surface of the epibranchiale in *Atrichornis* appears to be advanced.

Insertion of the M. tracherhyoideus, in part or completely, on the anterior end of the ceratobranchiale is found in a few passerine birds, e.g. *Corvus*, *Nucifraga* and other corvoids, and appears to be the primitive condition. In most passerines, most or all of the M tr hyoideus inserts on the cricoid, with few or no fibres extending to the ceratobranchiale; this appears to be the advanced condition. It is unclear whether a

ceratobranchial insertion of this muscle can reevolve once it has been lost. The condition in *Atrichornis* thus appears to be relatively primitive, but has almost reached the advanced stage seen in most other passerine birds.

The other tongue muscles in *Atrichornis* do not have a structure that can be assigned clearly to a primitive or an advanced state. In addition to the musculature, it should be mentioned that the flattened keel of the basihyale is most likely advanced compared to the cylindrical basihyale seen in most passerine birds.

Thus, *Atrichornis* possesses five aspects of the tongue musculature and one of the tongue skeleton which appear to be advanced, and one which is somewhat primitive. These advanced features of the tongue morphology are not consistent with the widely held belief (see Bock & Clench, 1985) that the *Menurae*, the suborder of suboscines to which *Atrichornis* has been placed, is a primitive group of passerine birds compared to the other oscines. Indeed, the tongue musculature of *Atrichornis* is remarkably advanced compared to that seen in most other genera of passerine birds which I have examined.

CONCLUSIONS

Skull morphology, namely the large free lacrymal that articulates with the frontal, provides some, but not very strong support for the generally accepted conclusion that *Atrichornis* is closely related to *Menura* (Bock & Clench, 1985). Little support exists from the osteology of the skull to support the hypothesis that these genera are closely related to *Menura* (Bock & Clench, 1985). Little support exists from the osteology of the skull to support the hypothesis that these genera are closely related to the bowerbirds (Ptilonorhynchidae). The morphology of the skeletomuscular system of the tongue suggests that *Atrichornis* has undergone considerable evolutionary change from the primitive passerine condition, but the functional and adaptive reasons for these advances are obscure.

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Systematic and Functional Aspects of the Locomotor System of the Scrub-birds, *Atrichornis*, and Lyrebirds, *Menura* (Passeriformes: Atrichornithidae and Menuridae)

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ABSTRACT. The forelimb and hindlimb musculature was dissected in the Noisy Scrub-bird, *Atrichornis clamosus* (Atrichornithidae), and the Superb Lyrebird, *Menura novaehollandiae* (Menuridae). The purposes of the study were to test certain phylogenetic hypotheses and to examine the locomotor specializations of the Menurae. The two families share derived myological traits and are sister groups. The structure of M. flexor perforatus digiti IV confirms that their affinities are with the oscines and not with the suboscines. The scrub-birds have the more highly derived limb morphology. The Menurae exhibit several myological conditions not shared with the Ptilonorhynchidae, other members of the 'corvid assemblage' or other passerines. They are, therefore, not similar to the bowerbirds in their limb musculature. A sister-group relationship with bowerbirds is not ruled out, however, because the peculiarities of the Menurae could have evolved after separation from a common ancestor with the bowerbirds, but the same is true for any suggested sister group.

Both scrub-birds and lyrebirds are nearly flightless. *Atrichornis* has reduced clavicles and greater forelimb reduction than does *Menura*. In contrast, *Menura* shows greater specialization in the hindlimb, which is elongated and has enlarged claws specialized for digging and grasping.

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KEYWORDS: Atrichornithidae, forelimb, hindlimb, Menuridae, Menurae, morphology, myology.

Two families of Australian passerines, the Menuridae (lyrebirds) and Atrichornithidae (scrub-birds), have puzzled systematists for over a century. While generally considered closely related to each other, their affinities to other birds have remained unclear. Although they bear little resemblance to suboscines, they have been classified as a suborder Menurae within the order Passeriformes (Wetmore, 1960). The question of their relationships was reopened by Sibley (1974) who studied the electrophoretic patterns of the egg-white proteins of *Menura* and reviewed other data, especially relating to anatomy and behaviour. He concluded that the Menuridae are oscine and are most closely related to the bowerbirds (Ptilonorhynchidae) and birds-of-paradise (Paradisaeidae) within a radiation of Australasian 'corvine' families. Because of the presumed relationship of the Atrichornithidae to the Menuridae, Sibley also suggested that the former family be placed next to the Menuridae in the suborder Passeres (oscines), although he did not study the proteins of the scrub-birds. Sibley (1974, 1976) reviewed the history of the problem.

More recently, Sibley & Ahlquist (ms.) reinvestigated this problem using the technique of DNA-DNA hybridization. Their study supported the sister-group relationship of the Atrichornithidae and Menuridae, and also indicated that these families are in turn most closely related to the Ptilonorhynchidae. Surprisingly, however, the Ptilinorhynchidae and Paradisaeidae were found to be widely separated on the basis of the DNA analysis, so Sibley no longer hypothesizes a close relationship of the birds-of-paradise with the lyrebirds and scrub-birds.

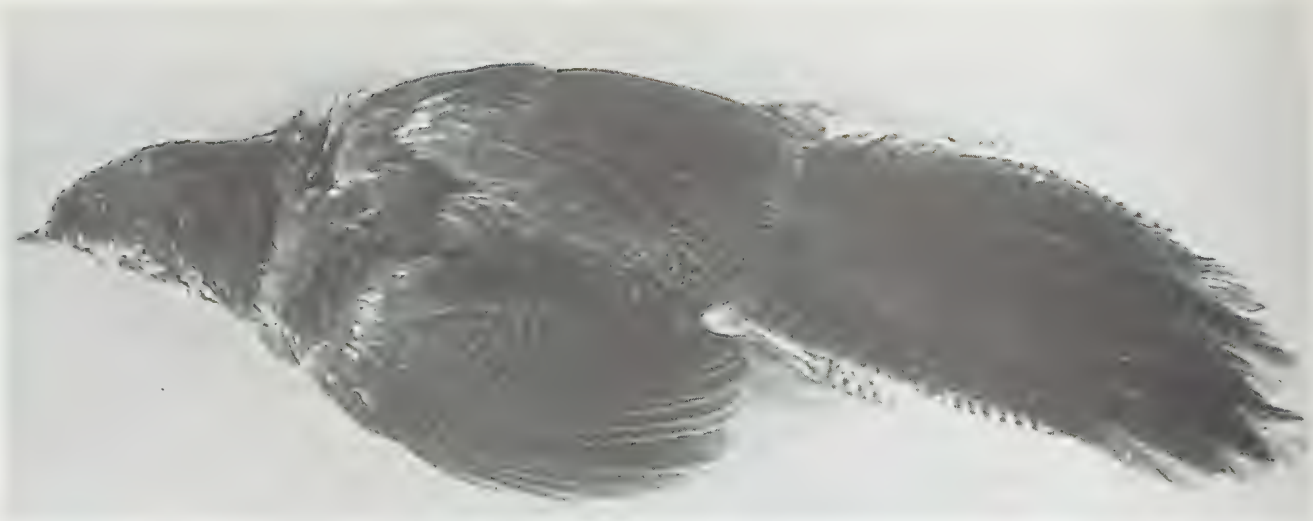

Fig. 1. Dorsal view of female Noisy Scrub-bird, *Atrichornis clamosus*, preserved specimen with feathers air-dried. Note the long, broad tail and the short, rounded wings.

The behaviour of the Menurae is likewise poorly known. Only brief observations on the locomotion of scrub-birds and lyrebirds have been reported. Both groups are ground-dwelling, forest inhabitants and forage for invertebrates in the leaf litter. Smith (1976) reported that the Noisy Scrub-bird (*Atrichornis clamosus*) does not use its feet when foraging, but Serventy (1966) cited a report that the Rufous Scrub-bird (*A. rufescens*) does scratch on the ground with its feet. This single report appears to be exceptional given the experience of other observers. The Superb Lyrebird (*Menura novaehollandiae*) actively uses its feet in foraging by raking the litter with its large claws and picking up branches to move them aside with its feet (Smith, 1968), and Albert's Lyrebird (*M. alberti*) forages in a similar manner (Robinson, 1976:333).

Both genera of the Menurae are nearly flightless. The Superb Lyrebird nests and roosts above the ground, climbing up through the trees by leaping zig-zag fashion from branch to branch, then gliding down to the nest (Smith, 1968). Mary H. Clench (pers. comm.) reported that a Superb Lyrebird flew from the ground to a branch about six feet high by leaping upward and flapping its wings strongly. Lyrebirds return to the ground by gliding downward and using the wings for braking (Smith, 1968). Little has been written about the flight of scrub-birds, but Jackson (1921) observed a Rufous Scrub-bird that he was pursuing fly (or at least flutter) for a distance of about ten feet at an altitude of one foot. Smith & Robinson (1976), however, reported that, although scrub-birds are primarily terrestrial, "they spend far more time in short flights in thick scrub than has previously been reported...". The wings of scrub-birds are very short and rounded, hardly reaching past the base of the long tail (Fig. 1).

In this paper I provide new information on the anatomy of the Menurae and comment on its relevance to the taxonomic and behavioural matters noted above. My study involved a dissection of the forelimb and hindlimb muscles of a lyrebird and a scrub-bird. The results are analyzed in relation to Sibley's hypotheses and also in comparison to other studies of passerine appendicular myology. Specifically, I address the following questions. (1) Are the Atrichornithidae and Menuridae most closely related to each other? (2) Are they oscine? (3) Are they closely related to the Ptilonorhynchidae or Paradisaeidae? (4) What are the morphological correlates of their locomotor specializations?

MATERIALS AND METHODS

The specimens dissected included an adult female Noisy Scrub-bird, *Atrichornis clamosus*, and an adult female Superb Lyrebird, *Menura novaehollandiae*. Some additional observations were made on an adult male Superb Lyrebird. Dissection was done with the aid of a stereomicroscope, the muscles being stained with iodine to enhance the clarity of the fibre arrangements. Comparisons with the myology of the Ptilonorhynchidae and Paradisaeidae are based on the work of Borecky (1977), who also provided helpful personal consultations. The drawings were made directly from specimens with the aid of a camera lucida microscope attachment. Anatomical nomenclature is based largely on the Nomina Anatomica Avium (Baumel *et al.*, 1979).

A functional comparison of the locomotor system may profitably include a study of the relative proportions of various parts. In order to make direct comparisons of birds of different sizes, ratios were calculated of various measurements relative to body weight. Linear measurements were compared to the cube root of weight in order to minimize the effect of different weights. These simple comparisons provide only a rough estimate of the relationship between linear dimensions and weight, but they are adequate to illustrate the deviation that the Menurae show from some 'typical' oscine bodily proportions.

In order to assess changes associated with the near loss of flight, a group of five species of oscines was chosen as a basis for comparison. These are all strong

fliers but are not highly specialized for any particular mode of flight, e.g., prolonged aerial hawking. The mean values of measurements of five species provide a rough model of a 'typical' oscine for comparison with the Menurae. *Atrichornis* lies within the range of weights of these five species, but *Menura* is much larger (Table 4).

The arcs of curvature of the claws were measured by the method used by Engels (1940) in measuring bill curvature.

The following abbreviations are used in the figure legends:

BB: M. biceps brachii
CC: M. coracobrachialis caudalis
CCR: M. coracobrachialis cranialis
CF: M. caudofemoralis
CL: clavicle
CO: coracoid
DM: a dermal muscle
DMA: M. deltoideus major
DMAC: M. deltoideus major pars caudalis
DMACR: M. deltoideus major pars cranialis
DMAP: M. deltoideus major proximal head
DMI: M. deltoideus minor
DP: deep dermal component of M. pectoralis
EMR: M. extensor metacarpi radialis
FCL: M. flexor cruris lateralis pars pelvica
FCLA: M. flexor cruris lateralis pars accessoria
FCM: M. flexor cruris medialis
FTED: M. femorotibialis externus pars distalis
FTEP: M. femorotibialis externus pars proximalis
FTI: M. femorotibialis internus
FTM: M. femorotibialis medius
GM: M. gastrocnemius pars intermedia
H: humerus
IC: M. iliotibialis cranialis
II: M. iliofemoralis internus
IL: M. iliotibialis lateralis
ISF: M. ischiofemoralis
ITC: M. iliotrochantericus caudalis
ITCR: M. iliotrochantericus cranialis
ITM: M. iliotrochantericus medius
LDC: M. latissimus dorsi pars caudalis
LDCR: M. latissimus dorsi pars cranialis
LDD: M. latissimus dorsi pars dorsocutaneous
OH: os humeroscapulare
OM: M. obturatorius medialis
P: M. pectoralis
PIF: M. pubo-ischio-femoralis
PIFC: M. pubo-ischio-femoralis pars cranialis
PIFCD: M. pubo-ischio-femoralis pars caudalis
RS: M. rhomboideus superficialis
S: scapula (Fig. 4), sternal carina (Fig. 9)
SBC: M. subcoracoideus
SC: M. supracoracoideus
ST: sternum
TB: M. triceps brachii
TH: M. humerotriceps
TPB: M. tensor propatagialis pars brevis
TPL: M. tensor propatagialis pars longa
TS: M. scapulotriceps.

MYOLOGY OF THE FORELIMB

A fully detailed description will not be given for each muscle because much of this would be a repetition of previous studies. Instead, I will compare each muscle with the descriptions for other passerines, especially the New World nine-primaried oscines (Raikow, 1977, 1978), the 'corvid assemblage' (Borecky, 1978) and the general review by Berger (1969), and will only comment on aspects in which the muscles of the Menurae differ from those descriptions, or on other points considered noteworthy. If no other comments are given, it may be assumed that the condition in the Menurae is similar to that in *Loxops virens* (Raikow, 1977) which is the reference species for comparison. If no distinctions are noted between them, then the condition is the same in *Menura* and *Atrichornis*.

The following muscles do not differ significantly from those in *Loxops virens* (Raikow, 1977) and require no discussion: Mm. rhomboideus profundus, scapulohumeralis cranialis, scapulohumeralis caudalis, subscapularis, coracobranchialis caudalis, sternocoracoideus, biceps brachii, brachialis, flexor digitorum superficialis, flexor carpi ulnaris, extensor metacapri radialis, extensor metacarpi ulnaris, extensor longus digiti majoris, ulnometacarpalis dorsalis, abductor alulae, adductor alulae, abductor digiti majoris, interosseus dorsalis, interosseus ventralis and flexor digiti minoris.

M. latissimus dorsi (Figs 2, 4). Both parts are present and entirely separate. Pars cranialis, a narrow, parallel-fibred muscle, arises from the dorsal midline superficial to M. rhomboideus superficialis and cranial to pars caudalis. It inserts fleshy on the proximodorsal surface of the humeral shaft caudal to the deltoid crest.

Pars caudalis is extremely large; a wide, flat, fan-shaped muscle arising fleshy from most of the dorsal midline of the thorax and also by a wide aponeurosis from the midline, which gives rise to three distinct caudal heads whose fleshy portions begin more distally. The entire muscle converges on a stout tendon of insertion that arises along its lateral border. It inserts on the caudodorsal surface of the humerus at the level of M. scapulohumeralis cranialis, the tendon inserting between fascicles of the humerotriceps. In *Menura*, pars caudalis is not as distinctly divided into heads caudally as it is in *Atrichornis*. A cutaneous component, M. latissimus dorsi interscapularis (dorsocutaneous), is also present (Fig. 2).

The form of pars caudalis, greatly enlarged and with an extensive area of origin, appears to be unique among passerines as far as known. It does not occur in the Paradisaeidae or Ptilonorhynchidae (Borecky, 1977). This condition is apparently a specialization of the Menurae, that is, a synapomorphy linking the two families.

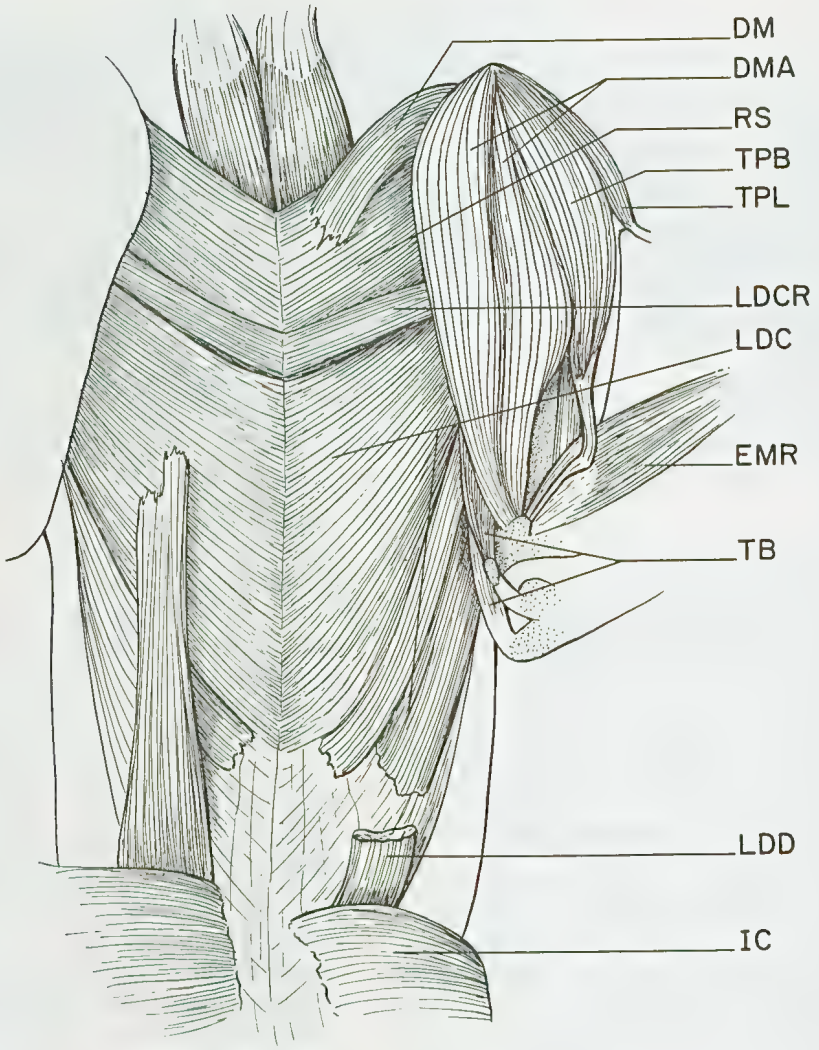

Fig. 2. Dorsal view of the muscles of the back and upper arm of *Atrichornis clamosus*. The greatly enlarged M. latissimus dorsi pars caudalis (LDC) is a synapomorphy of the Menurae. For abbreviations see Materials and Methods.

M. rhomboideus superficialis (Figs 2, 4). This muscle arises from the dorsal midline and converges slightly toward a fleshy insertion on the dorsomedial surface of the cranial half of the scapula; a few fascicles just reach the medial surface of the head of the clavicle.

M. serratus profundus. The two large cranial bellies are entirely separate.

M. serratus superficialis. This is of normal passerine form. I did not find pars costohumeralis in *Atrichornis*, but it was probably removed during prior skinning. Pars costohumeralis was present in *Menura*.

M. subcoracoideus (Fig. 5) In *Menura,* the dorsal head arises only from the scapula, while in *Atrichornis* a few fascicles also arise from the adjacent ventral margin of the head of the clavicle.

M. pectoralis (Figs 3, 5, 8, 9). In *Atrichornis,* the belly (pars thoracicus) is relatively small in association with reduced flying ability. It has a normal area of origin from the sternal plate and carina, and the membrane overlying the sternal ribs. As discovered by Garrod (1876) in *Atrichornis rufescens,* the distal 60% of the clavicle is absent, only the head and a short shaft remaining. Only a few fibres of the pectoralis arise from the clavicle; the muscle mainly attaches around the bone, arising from both the cranial and caudal surfaces of the coracoclavicular membrane. A dermal component arises from the deep surface. In *Menura,* pars thoracicus is also reduced in size but retains a normal origin from the areas noted above and also from the ventral, caudal and dorsal surfaces of the clavicle (which is complete) in the usual manner. Near the insertion there is a wide tendinous connection from the deep surface of the muscle to the origin of the M. biceps brachii. Pars propatagialis longus is fleshy in *Loria* and *Semioptera* (Paradisaeidae) and *Amblyornis* (Ptilonorhynchidae). In the other bowerbirds and birds-of-paradise, and in the Corvidae, Callaeidae, Grallinidae and Cracticidae, it is tendinous (Borecky, 1977), as in the Menuridae and Atrichornithidae.

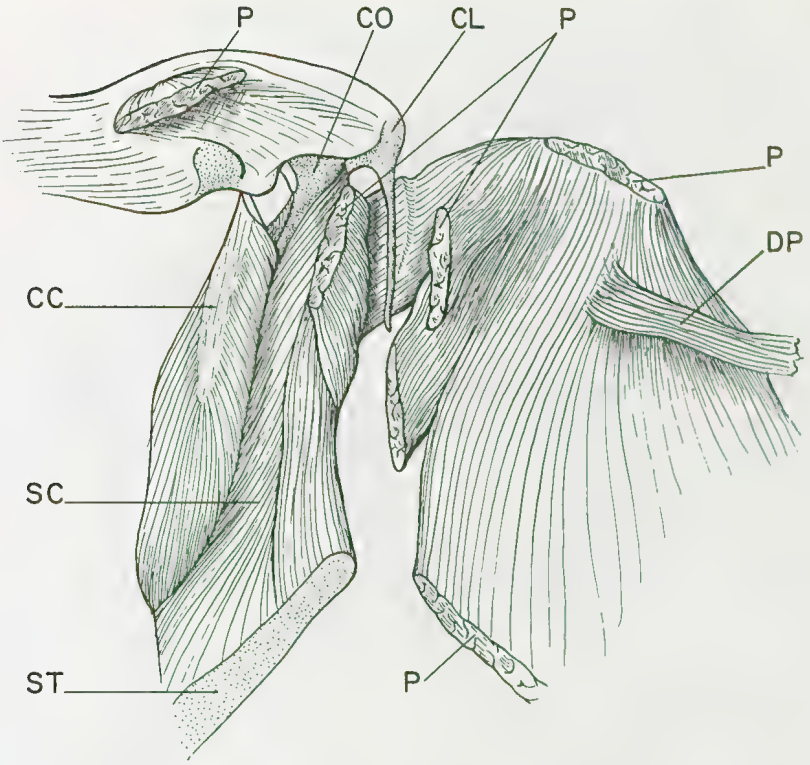

Fig. 3. Ventrolateral view of the deep muscles of the shoulder region in *Atrichornis clamosus*. The M. pectoralis has been cut free in several places (P) and reflected to the right, showing how the vestigial shaft of the clavicle lies essentially free within the belly of the muscle. For abbreviations see Materials and Methods.

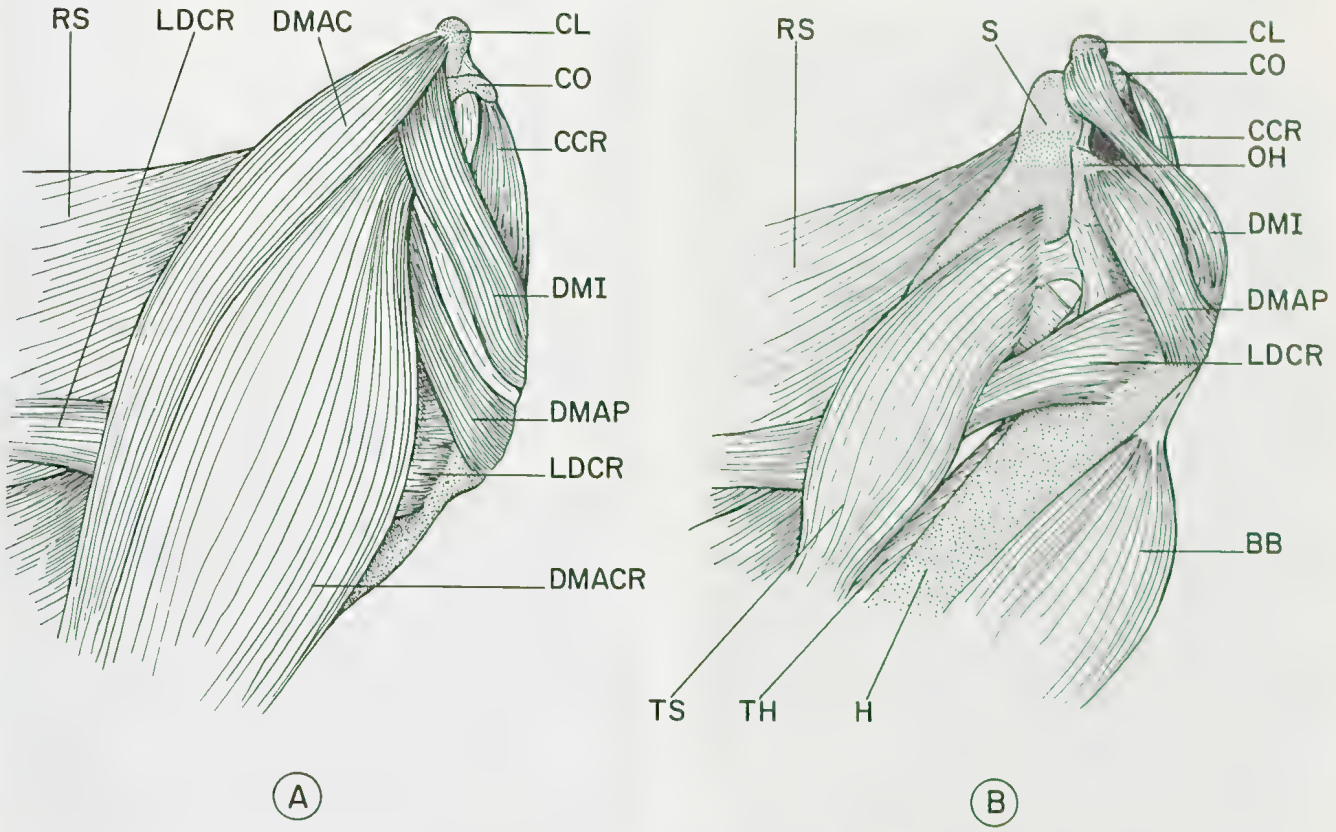

Fig. 4. Dorsal views of the shoulder muscles in *Atrichornis clamosus*. A, Superficial muscles. B, Deeper muscles after removal of M. deltoideus major, and rotated somewhat to the left. For abbreviations see Materials and Methods.

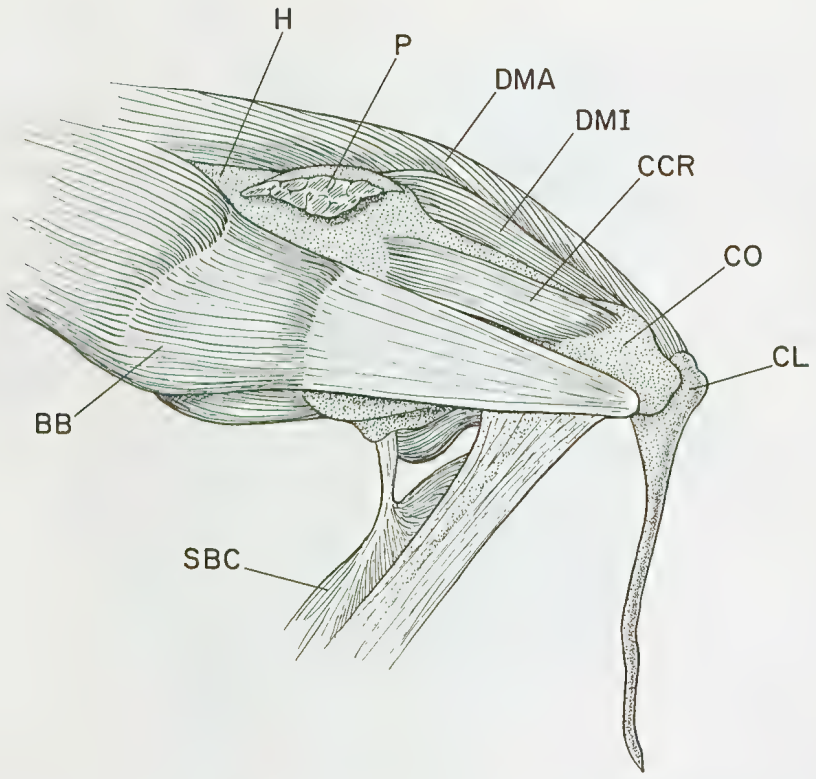

Fig. 5. Craniolateral view of the deep shoulder muscles in *Atrichornis clamosus*, also showing the vestigial form of the clavicle, with a well developed head but a short and attenuated shaft. For abbreviations see Materials and Methods.

M. supracoracoideus (Figs 3, 9). This bipennate muscle is reduced in size from that expected in a bird of comparable size but normal flying ability. In *Menura,* it arises fleshy from the dorsolateral surface of the cranial ⅔ of the sternal carina, the adjacent sternal plate, the cranioventral surface of the sternum, a small area on the cranioventral surface of the coracoid and cranioventrally from a midsagittal sternoclavicular membrane and the coracoclavicular membrane, all deep to the M. pectoralis. The origin of the muscle in *Atrichornis* is similar, but the muscle is relatively more reduced than in *Menura* and arises only from the cranial ½ of the sternal carina (compared to ⅔ in *Menura*). Also, in *Atrichornis,* the origin of the muscle does not extend cranially beyond the end of the sternum, as in *Menura*, because there is no discernible sternoclavicular membrane in *Atrichornis*.

M. coracobrachialis cranialis (Figs 4, 5). This is a small but fully developed muscle with normal muscle tissue; it has not degenerated to connective tissue as in many passerines. The parallel-fibred belly arises by a short tendon from the lateral surface of the head of the coracoid and passes across the shoulder joint to insert fleshy on the proximal end of the humerus, just ventral to the proximal end of the pectoral crest, between the latter and the coracoidal tendon of M. biceps brachii, and along its edge deep to the latter.

M. cucullaris capitis pars propatagialis. I did not find this muscle in either of the Menurae examined. However, it may have been removed during prior skinning and so should not necessarily be considered absent.

M. tensor propatagialis (Fig. 2). Pars longa and pars brevis are separate as in other passerines. Garrod (1876) reported that in *Menura superba*(= *novaehollandiae*) and *Atrichia* (=*Atrichornis*) *rufescens* the tendon of insertion of pars brevis differs from that in most passerines. Typically, this tendon passes to the dorsal surface of the belly of M. extensor metacarpi radialis is attached there, and then turns to run parallel to the long axis of the muscle to an insertion on the ectepicondylar process of the humerus, near the elbow. In doing so, it runs roughly parallel to the tendinous origin of the M. extensor metacarpi radialis, but is separate from it. Garrod reported that in the Menurae he dissected, the tendons of the two muscles were fused together for their entire length, as also occurs in some Piciformes. My dissection confirms this for *Menura*, but in *Atrichornis clamosus* I found the two tendons to be separate in the usual passerine manner.

M. deltoideus major (Figs 2, 4, 5). This muscle occupies the dorsal surface of the forearm. At its proximal end it lies deep to M. tensor propatagialis pars longa. It is divided into two separate bellies, par cranialis and pars caudalis, which are of normal form in most respects. However, pars cranialis in *Menura* has an unusual proximal head that is continuous with the main part of the belly, but demarcated from it by a fairly

distinct plane of separation, and arising from the os humeroscapulare. In *Atrichornis,* this proximal portion has become clearly separated from the main part of pars cranialis, a distinct gap seperating the insertions of the two parts. In this characteristic, then, *Atrichornis* is more highly derived than is *Menura*. This separate proximal head does not occur in other passerine birds so far as known.

M. deltoideus minor (Figs 4, 5). In *Atrichornis,* this small, strap-shaped, parallel-fibred muscle lies cranioproximal to M. deltoideus major and caudal to M. coracobrachialis cranialis. It arises fleshy from the apex of the coracoid and slightly from the coracoclavicular ligament, a few fascicles perhaps also arising from the acromion of the scapula. The muscle passes distally, superficial to the supracoracoideus tendon to insert fleshy on the pectoral crest of the humerus just distal to the insertion of the supracoracoideus tendon. *Menura* is like *Atrichornis*, but it is more apparent that a few fascicles do arise from the acromion. This muscle is unusual in the Menurae in that it arises almost exclusively from the coracoid, with hardly any origin from the scapula. In the New World nine-primaried oscines, it arises either from the scapula alone, or from the scapula and coracoid (Raikow, 1978). The muscle arises from the scapula alone in the Sturnidae, Callaeidae, Cracticidae, Corvidae, Paradisaeidae (except *Loria*), and *Grallina* and *Struthidia* (Grallinidae). It arises from both the scapula and coracoid in *Corcorax* (Grallinidae), *Loria* and the Ptilonorhynchidae (Borecky, 1977). In the latter case there is an extensive origin from the scapula, unlike the very small origin in the Menurae. Thus, the peculiar form of this muscle does not support a relationship of the Menurae with the Ptilonorhynchidae or Paradisaeidae.

M. triceps brachii (Figs 2, 4). The scapulotriceps cannot be divided into two parts as in some passerines (Raikow, 1978). Distally, several fascicles of the humerotriceps contribute to the insertion of the scapulotriceps.

M. expansor secundariorum. This muscle is of normal passerine form in *Atrichornis*, including its insertion onto three secondaries. In *Menura*, however, it inserts onto the innermost four secondaries.

M. pronator superficialis. The belly extends for most of the length of the radius, inserting near the wrist.

M. pronator profundus. This muscle originates from the distal end of the humerus and from the adjacent humeroulnar pulley. It is the same in both genera. It spreads out to an extensive line of attachment along the shaft of the radius. Two distinct forms have been described in passerines. In one, the muscle is fan-shaped and single, with a continuous line of insertion. In the second, the muscle is divided into two distinct bellies, one inserting proximally and one distally on the radius; the two insertions are separated by a clear gap. Intermediate conditions sometimes occur. The undivided form is considered primitive in passerines and the divided form derived (Raikow, 1978; Bentz, 1979). The condition in the Menurae is single and undivided, as it is in the 'corvid assemblage'.

M. flexor digitorum profundus. This muscle is of normal form in the Menurae. The two heads originate adjacent to the entire length of the area of insertion of the M. brachialis.

M. ulnometacarpalis ventralis. This is of normal form in the Menurae. It arises by a shallow V-shaped origin, the caudal arm being longer than the cranial arm.

M. extensor digitorum communis. The belly extends almost the entire length of the forearm, but is slightly shorter than the underlying M. extensor longus digiti majoris and M. extensor metacarpi ulnaris. The proximal branch of the tendon of insertion inserts on the base of the dorsal surface of the alular digit; it does not branch as in the New World nine-primaried oscines (Raikow, 1977).

M. ectepicondylo-ulnaris. The belly extends about ⅔ the length of the ulna, compared to about ⅓ in the 'corvid assemblage' (Borecky, 1977).

M. supinator. This muscle inserts along the proximal ½ of the radius, whereas in the 'corvid assemblage' it inserts on the proximal ¼ (Borecky, 1977).

M. extensor longus alulae. As in other passerines there is only an ulnar head, no radial head occurs. The tendon of insertion fuses with that of the M. extensor metacarpi radialis a short distance before their common insertion.

MYOLOGY OF THE HINDLIMB

The format of the muscle descriptions is the same as that used for the forelimb. The basis of comparison is with the hindlimb muscles of *Loxops virens* (Raikow, 1976). Mm. femorotibialis medius, extensor digitorum longus, fibularis longus and lumbricalis are present in normal form and require no discussion.

M. iliotibialis cranialis (Figs 2, 7). In *Atrichornis,* this muscle arises from the median dorsal ridge of the cranial end of the pelvis, mainly fleshy but by a short aponeurosis at its caudal end. There is one head, lying superficial to the M. iliotrochantericus caudalis, and entirely cranial to the M. iliotibialis lateralis. The cranial end of the M. iliotrochantericus caudalis lies medial to this muscle. In *Menura*, the origin is quite different: slightly from the median dorsal ridge cranially, but mainly from the cranial edge of the ilium, partly medial to the M. iliotibialis lateralis and M. iliotrochantericus caudalis; the latter does not extend over the medial surface of the muscle as in *Atrichornis*. The origin in *Menura* is thus longer than in *Atrichornis*, the muscle as a whole being relatively larger. This origin is of typical passerine form, that of *Atrichornis* being rather more restricted in area. In both genera, the insertion lies deep to the patellar band of M. gastrocnemius.

M. iliotibialis lateralis. There are complete preacetabular, acetabular and postacetabular portions; no reduction of this muscle occurs as in some

passerines. The origin extends caudally slightly farther in *Menura* than in *Atrichornis*. In the former it lies superficial to the caudal edge of the M. flexor cruris lateralis, while in the latter it reaches only the cranial edge of that muscle. M. iliotibialis lateralis is well developed in both genera, and especially in *Menura* is quite massive and thick. The proximal and distal aponeurotic regions are of normal passerine form.

M. iliofemoralis externus. This muscle is absent in *Atrichornis* and *Menura*. In many nonpasserine birds it arises from the cranial iliac crest just caudal to M. iliotrochantericus caudalis, and in some cases is fused in part to the latter muscle. Its tendon passes distally over the lateral surface of the trochanter of the femur and inserts in some cases distal, but more commonly proximal, to the tendon of insertion of M. ischiofemoralis (references in George & Berger, 1966: 393). Until recently, this muscle was considered lacking in passerines, though it has been found as a developmental anomaly (Raikow, 1975; Raikow *et al.*, 1979). However, Borecky (1977) found the M. iliofemoralis externus to be present in the Callaeidae and Ptilonorhynchidae, where its belly is partly fused to that of the M. iliotrochantericus caudalis, but partly free and with an entirely separate tendon of insertion. In *Turnagra* (now considered to be a paradisaeid by Olson *et al.*, 1983) and in the primitive bird-of-paradise *Loria,* the muscle is also present, its belly fully fused to that of the M. iliotrochantericus caudalis, but still with a separate tendon. Among the Paradisaeidae, *Epimachus* had a condition like that in the Ptilonorhynchidae, while in seven other genera the situation is difficult to interpret. There is no apparent M. iliofemoralis externus, but the M. iliotrochantericus caudalis extends caudally slightly farther than in most passerines, and Borecky (1977) suggested that this might represent a complete fusion of the M. iliotrochantericus caudalis and the M. iliofemoralis externus.

The condition in the Menurae is like that in most paradisaeids, that is, there is no M. iliofemoralis externus, but the M. iliotrochantericus caudalis is extensive. Thus, the condition in the Menurae is unlike that in the Ptilonorhynchidae or in *Loria* or *Epimachus*, but is similar to that in most birds-of-paradise. At my request, Dr Borecky examined the specimens of the Menurae, and felt that the caudal extent of the M. iliotrochantericus caudalis was not as pronounced as in the birds-of-paradise, although this is admittedly a subjective judgement. The problem is that the resemblance could be due either to a shared primitive condition or to a shared derived condition, but we lack the information necessary to choose between these possibilities. Considering the condition in the Ptilonorhynchidae, *Loria* and *Epimachus*, however, we may at least conclude that this character fails to support a relationship between the Menurae and the bowerbirds and primitive birds of paradise, and perhaps also the typical birds of paradise.

M. iliotrochantericus caudalis (Fig 6). This muscle is

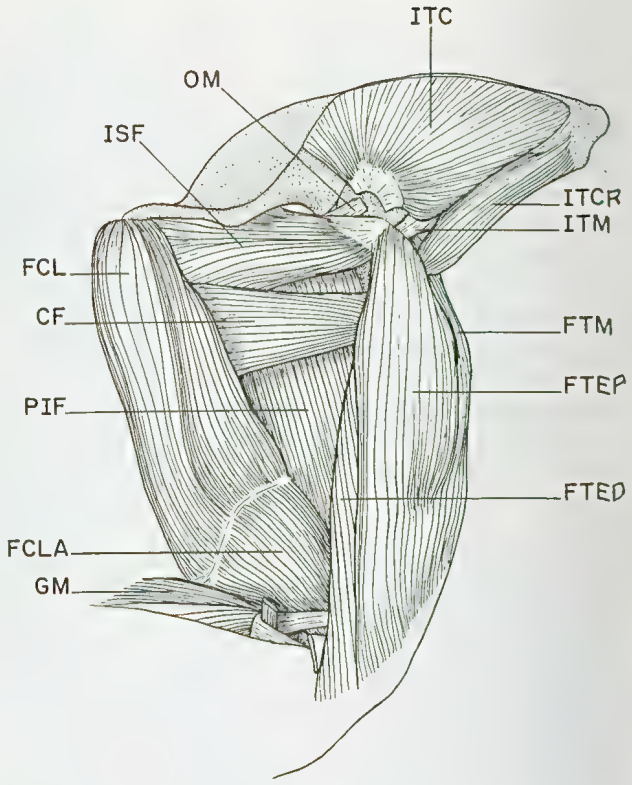

Fig. 6. Lateral view of the thigh muscles in *Atrichornis clamosus* after removal of the more superficial muscles M. iliotibialis cranialis, M. iliotibialis lateralis and M. iliofibularis. For abbreviations see Materials and Methods.

of normal form in the Menurae, but quite well developed with a full cranial margin that curves ventrally and then back up to the tendon of insertion. Caudally, in *Menura* a part of the belly is partially separate, which could be interpreted as a fused belly of the M. iliofemoralis externus, but is actually due to a fascial plane accompanying the point of entry of a nerve, and commonly seen as an artifact of dissection. See discussion under M. iliofemoralis externus.

M. iliotrochantericus cranialis (Figs 6, 7). This is of normal form. It inserts on the craniolateral surface of the femur, on a raised tubercle in *Atrichornis* and on a well developed ridge (iliotrochanteric tuberosity) in *Menura*.

M. iliotrochantericus medius (Fig. 6). This is of normal form and quite well developed. It arises on the lateroventral surface of the pelvis, cranial to the acetabulum, and lies lateral to M. iliofemoralis internus.

M. femorotibialis externus (Fig. 6). A deep distal head (pars distalis) is present , arising proximally at the level of insertion of the M. caudofemoralis on the femur. It is almost entirely separate from pars proximalis. The M. femorotibialis externus is much more distinctly separate from the adjacent M. femorotibialis medius than in the Paradisaeidae, Ptilonorhynchidae or other passerines studied. The two muscles are separated by a deep cleft in the proximal half of the thigh. Distally,

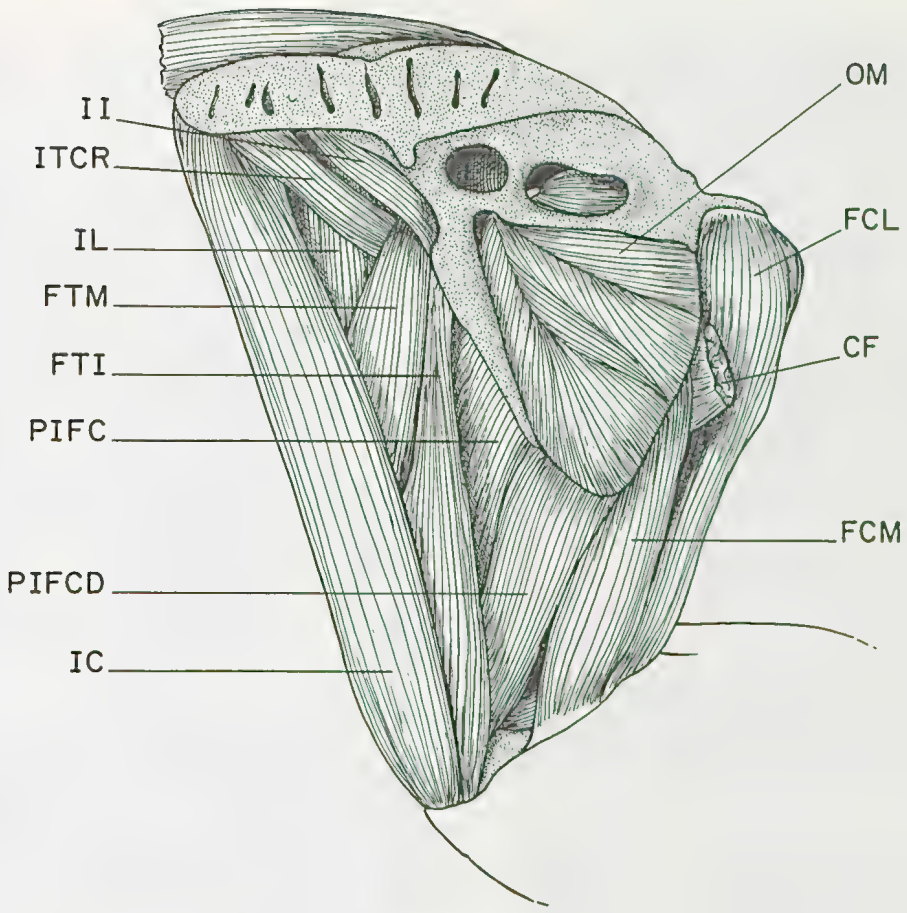

Fig. 7. Muscles on the medial surface of the thigh in *Atrichornis clamosus*. The expanded, doubly bipennate form of the M. obturatorius medialis (OM) is a synapomorphy of the Menurae. For abbreviations see Materials and Methods.

however, they merge in a way that makes separation arbitrary.

M. femorotibialis internus (Fig. 7). In many passerines, including the Ptilonorhynchidae, Paradisaeidae and Corvidae (Borecky, 1977), this muscle is divided into two heads with separate tendons of insertion. In the Menurae, however, there is only a single head and tendon.

M. iliofibularis. This muscle is generally of normal form, but more narrow than usual. It arises mainly fleshy along the dorsolateral iliac crest, and by a narrow aponeurosis at its cranial end from the deep surface of the overlying M. iliotibialis lateralis. The dorsolateral iliac crest projects laterally to an unusual degree, with the muscle arising fleshy from its ventral surface. The muscle then is fairly thick, and thus relatively massive despite its narrowness in the cranial-caudal dimension. Because the belly is narrow, the line of origin does not extend caudally as far as the cranial margin of the M. flexor cruris lateralis, but instead a small gap separates the two muscles at their origins.

M. flexor cruris lateralis (Figs 6, 7). This muscle is massively developed in the Menurae. It arises mainly fleshy from the caudal end of the ilium which projects caudally as a bony projection, a continuation of the caudolateral iliac crest. The muscle arises from the lateral, caudal and medial surfaces of this projection. This origin is different from that in the Ptilonorhynchidae, Paradisaeidae and most other passerine birds described, in that there is no aponeurotic origin from the caudal vertebrae. A similar condition exists, however, in many of the furnarioid or 'tracheophone' passerines (Raikow, unpubl. obs.). The belly passes distally to a raphe separating the proximal portion just described, pars pelvica, from the distal portion, pars accessoria. The raphe extends medially to fuse with the lateral surface of the distal end of M. flexor cruris medialis, contributing to the latter's tendon of insertion. It is also rather loosely joined to the adjacent M. gastrocnemius pars intermedia. Pars accessoria inserts fleshy on the femur in the popliteal area and on the shaft proximal to this and lateral to M. pubo-ischio-femoralis pars cranialis and medial to the biceps loop (ansa M iliofibularis).

M. caudofemoralis (Figs 6, 7). The attachment to the femur and form of the belly are normal. The attachment to the pygostyle was not observed. The belly is relatively wider in *Atrichornis* than in *Menura*.

M. ischiofemoralis (Fig. 6). This is of normal form in the Menurae. The area of origin is more extensive in *Atrichornis*, beginning dorsally just under the caudolateral iliac crest, while in *Menura* it arises only from the lateral surface of the ischium, its dorsal margin beginning even with the dorsal margin of the ilioischiatic fenestra.

M flexor cruris medialis (Fig. 7). In *Atrichornis*, the

origin begins just caudal to that of the M. pubo-ischio-femoralis pars cranialis, while in *Menura* it is separated from that muscle by a gap of about 1 cm.

M. pubo-ischio-femoralis (Figs 6, 7). Pars cranialis is normal. In other passerines, the insertion of pars caudalis fuses with the origin of M. gastrocnemius pars intermedia, but in *Menura* these muscles are entirely separate, while in *Atrichornis* they are only slightly fused.

M. obturatorius lateralis. Pars ventralis is of normal form. Pars dorsalis is exceedingly small. It arises from the ischium just dorsal to the obturator foramen, passes craniolaterally dorsal to the tendon of M. obturatorius medialis and inserts on the head of the femur just distal to that tendon, which it overlies slightly. The muscle has no origin from the ventral edge of the ilioischiatic fenestra. In *Atrichornis*, it consists of only a few fascicles, being practically absent. This is in great contrast to the condition in the Paradisaeidae, Ptilonorhynchidae and their allies (Borecky, 1977), where the muscle is very large, arising along nearly the entire ventral margin of the ilioischiatic fenestra. Furthermore, in those groups, the muscle inserts in part on the tendon of the M. obturatorious medialis and in part on the femur, rather than just on the femur as in the Menurae.

M. obturatorius medialis (Figs 6, 7). This triangular muscle is of unusual form in the Menurae. It is distinctly wider in dorsoventral dimension than is typical for passerines, including the bird-of-paradise assemblage (Borecky, 1977; pers. comm). From the medial aspect, its fibre arrangement is divided into two bipennate portions converging on the tendon of insertion, one dorsal and one ventral. Although this muscle is often divided into two bipennate regions, this is usually not visible from the medial surface. In the Paradisaeidae and allies, the medial aspect shows a simple bipennate pattern.

M. iliofemoralis internus (Fig. 7). This muscle arises fleshy from the ventrolateral surface of the ilium, just cranial to the acetabulum and caudal to the origin of M. iliotrochantericus cranialis. It inserts fleshy on the caudomedial surface of the femur. The muscle lies medial to M. iliotrochantericus medius. In *Atrichornis*, the cranial edge of the muscle is even with that of M. iliotrochantericus medius, while in *Menura* it originates slightly cranial to the cranial edge of that muscle. This is in contrast to the Paradisaeidae and Ptilonorhynchidae, in which M. iliofemoralis internus arises caudal to M. iliotrochantericus medius (Borecky, 1977).

M. gastrocnemius. Pars lateralis is of normal form in both genera and extends about ⅔ the length of the shank. Pars intermedia is of normal form. It extends about half the length of the crus in *Menura* and about ⅓ this distance in *Atrichornis*. Pars medialis has a well developed superficial head and a patellar band in both species, and is therefore Type 1 (Raikow, 1978). In *Atrichornis*, the patellar band does not quite reach the patella, covering 0.80 of the patellar ligament, while in *Menura* it does reach the ventral edge of the patella (1.00). This is like the condition in the Ptilonorhynchidae, Paradisaeidae and most of the 'corvid assemblage' (Borecky, 1977), but as it is probably a primitive state in the oscines it is of little taxonomic significance.

M. tibialis cranialis. This is of normal form in the Menurae and extends about ¾ the length of the crus.

M. fibularis brevis. This is of normal passerine form in *Menura*. In *Atrichornis*, the origin extends slightly proximal to the level of the M. iliofibularis tendon, but there is no tibial head as in the Drepanididae (Raikow, 1976).

M. flexor perforans et perforatus digiti III. This muscle extends about ⅔ the length of the crus. It is bipennate for its entire length, unlike the condition in the New World nine-primaried oscines (Raikow, 1976, 1978) and the bowerbird group (Borecky, 1977), where the proximal part is bipennate and the distal part is unipennate.

M. flexor perforans et perforatus digiti II. This muscle is of normal form, including a partial origin from the adjacent M. flexor perforans et perforatus digiti III. It extends ½ the length of the crus in *Atrichornis* and ¾ in *Menura*. At its insertion, the tendon ensheathes that of the M. flexor digitorum longus, which is the primitive state (Borecky, 1977).

M. flexor perforatus digit IV. In *Menura*, this arises by a tendon from the intercondyloid region in common with M. flexor perforatus digiti III and the medial head of M. flexor hallucis longus. In *Atrichornis*, the origin is similar but is partly fleshy. The structure of this muscle corroborates Sibley's hypothesis of oscine affinities for the Menurae. In dissections of many oscine and suboscine groups, I have found that this muscle has three distinctively different forms among the passerine birds. In Type 1, the muscle has two separate bellies: a lateral belly arising near the proximal end of the crus mainly from the head of the fibula, and a medial belly arising from the intercondyloid region of the femur. These bellies give rise to separate tendons that pass distally, fusing into a single tendon just before entering the tibial cartilage at the intertarsal joint. This type was found in the Pittidae, Philepittidae, Furnariidae, Formicariidae, Dendrocolaptidae, Rhinocryptidae and some species of Eurylaimidae. Because this condition is similar to that in most nonpasserine birds, and because the order Passeriformes is monophyletic (Raikow, 1982), outgroup comparison indicates that Type 1 is primitive among passerines. Type 2 is different, having two bellies but with a single tendon. Variants of this type occur in the Tyrannidae, Cotingidae and Pipridae, and in some Eurylaimidae. These are derived states in the passerines. The third major variation in M. flexor perforatus digiti IV is Type 3, in which only the medial belly is present, and no lateral component of any sort occurs. This is a derived state that helps to define the oscines as a clade. The

Menurae have this condition, which confirms that they are part of a clade with the oscines, but does not itself indicate anything about their relationship to any particular oscine group.

M. flexor perforatus digiti III. This muscle is of normal passerine form; as in other birds its tendon is joined by the long branch of the tendon of insertion of M. fibularis longus. The muscle arises by a long tendon from the intercondyloid region of the femur in common with M. flexor perforatus digiti IV; this tendon is separate from the origin of M. flexor hallucis longus. In *Menura* the belly does not extend as far caudally as does that of M. flexor perforatus digiti IV, while in *Atrichornis* it extends farther caudally than the latter.

M. flexor perforatus digiti II. This muscle is of normal passerine form. At its insertion, the tendon is not bifurcate and is not perforated by the tendons of Mm. flexor perforans et perforatus digiti II and flexor digitorum longus. In the Paradisaeidae and most Ptilonorhynchidae (Borecky, 1977), it is bifurcate and perforated.

M. plantaris. This is of normal form in the Menurae. It extends about ¼ the length of the crus in *Menura* and slightly less in *Atrichornis*.

M. flexor hallucis longus. This muscle arises by three heads, as in passerines generally. The lateral head arises from the lateral femoral condyle by a tendon shared with M. flexor perforatus digiti II, as in other passerines. The intermediate head has a fleshy origin from the medial intercondyloid region of the femur, just lateral to the tendon of origin of the medial head. It is large in *Menura* and smaller in *Atrichornis*. In contrast, this head arises by a tendon in the Paradisaeidae and relatives (Borecky, 1977) and other passerines (Raikow, 1978). The medial head arises by a tendon in common with M. flexor perforatus digiti III and M. flexor perforatus digiti IV in the Menurae, while in other passerines this origin is fleshy.

M. flexor digitorum longus. In the Menurae, this muscle arises by two heads, one from the fibula and one from the tibiotarsus, as in most birds. In the Corvidae and Paradisaeidae (except *Loria*), there is a third head from the intercondyloid region of the femur. This is lacking in the Ptilonorhynchidae.

M. flexor hallucis brevis. This small muscle of the foot is of normal size in the Menurae, while in the Paradisaeidae and Ptilonorhynchidae it is enlarged compared to most passerines (Borecky, 1977).

M. extensor hallucis longus. This is of normal form, though quite slender. A distal head was observed in *Atrichornis*, but could not be discerned in *Menura*.

SYSTEMATIC CONCLUSIONS

Most of the forelimb muscles of the Menurae are of typical oscine form. Where unusual conditions occur, the two genera are usually similar, so that the forelimb myology confirms their close relationship. The major differences between the Menurae and the Ptilonorhynchidae and Paradisaeidae are summarized in Table 1. Some of the peculiarities of the Menurae are clearly correlated with their near loss of flight; certainly this is the explanation for the reduced size of the M. pectoralis and M. supracoracoideus, and for the reduction of the clavicle in *Atrichornis*. In these respects *Atrichornis* is more highly derived than is *Menura*. The forearm muscles of the Menurae are relatively longer than those of the bowerbirds and birds-of-paradise, mostly reaching nearly the whole length of the forearm. However, in the Menurae, the forelimb skeleton is shortened relative to strongly flying birds (see below).

Other peculiarities of the forelimb muscles in the Menurae are more difficult to explain. The enlarged M. latissimus dorsi pars caudalis and the development of a proximal head in the M. deltoideus major differ from the condition in passerines generally. Thus, it is difficult to assess their significance relative to the Sibley and Ahlquist hypothesis. They are probably synapomorphies of the Menurae that developed after separation from their common ancestor with their closest relatives, whether these are the bowerbirds or some other group. The presence of a well developed M. coracobrachialis cranialis is not an indication of affinity between the Menurae and the bowerbirds as it is a primitive character state in the Passeriformes.

The hindlimb muscles give a similar picture (Table 2). Several muscles are distinctly different, not only from the bowerbird group, but from passerines generally; these include the M. femorotibialis externus, M. flexor cruris lateralis, M.obturatorius medialis, M. flexor perforans et perforatus digiti III and M. flexor hallucis longus. Other muscles show character states found in some other passerines, but differing significantly from the bowerbirds and birds-of-paradise; these include the M. femorotibialis internus, M. obturatorius lateralis pars dorsalis, M. iliofemoralis internus, M. flexor perforatus digiti II, M. flexor digitorum longus (in part) and M. flexor hallucis brevis. Again, these are not readily explained by reference to the near loss of flight in the Menurae.

Based on the preceding discussion and the differences noted in Tables 1 and 2, it is clear that the appendicular myology does not support the hypotheses (Sibley, 1974, 1976; Sibley & Ahlquist, ms.) that the Menurae are closely allied to the Ptilonorhynchidae or Paradisaeidae, but shows that they are structurally quite different. It is important here to clarify the possible meaning of 'relationship'. Phenetically, the two groups are quite dissimilar, but in cladistic or historical terms the problem is not degree of similarity, but recency of common ancestry. Sibley & Ahlquist hypothesize that the Menurae and Ptilonorhynchidae are sister groups, that is, that they share a more recent common ancestry with each other than with any other group. The Menurae possess a number of distinctive myological conditions not otherwise known in passerines, and therefore it is impossible to suggest another group with which they might share a more recent common ancestry than with the bowerbirds. It is possible that the

peculiarities of the Menurae arose after their separation from a common ancestry with the bowerbirds, but this could also be suggested for other possible sister groups. Thus, the limb muscle characters of the Menurae neither corroborate nor refute the hypothesis that the Menurae are most closely related to the Ptilonorhynchidae. Other systems may provide data showing such a relationship; such similarities will be most convincing if they constitute shared derived character states.

The appendicular myology strongly corroborates the close affinity of the Atrichornithidae and Menuridae. Some muscles differ slightly in size or proportions, generally those of the Menuridae being relatively larger in association with the lyrebirds' greater body size. Several differences may be noted (Table 3). These are minor compared to the distinctive and apparently synapomorphous similarities shared with no other known taxa. In addition, the M. flexor perforatus digiti IV, as discussed above, clearly confirms the affinity of the scrub-birds and lyrebirds with the oscines.

Considering their large size and specialized plumages, the Menuridae might be regarded as more highly derived than the Atrichornithidae, with their more typical passerine body size and nondescript plumage. In terms of limb morphology, however, the scrub-birds are the more advanced of the two families. This is seen in their more greatly reduced flight muscles (see below), the reduction of the clavicle and loss of the clavicular origin of the M. pectoralis, the greater separation of the proximal head of the M. deltoideus major pars cranialis, and the reduced extent of the origin of the M. iliotibialis cranialis.

FUNCTIONAL ANATOMY OF THE FORELIMB

Pectoral muscles. Reduction in the size of the pectoral muscles commonly accompanies the loss of flight in birds. I divided the wet weight of the paired muscles by the weight of the bird recorded before preservation. This value is the percent-weight of the muscle. The M. pectoralis provides the force for the downstroke or power stroke in flight, while M. supracoracoideus provides the upstroke or recovery stroke. Detailed descriptions of these muscles are given above. Table 4 shows that these muscles are reduced to less than half their 'normal' size in the Menurae, and are more reduced in *Atrichornis* than in *Menura*. The extent of the area of origin of both muscles is also reduced in *Atrichornis* compared to *Menura*. The reduction in *Atrichornis* especially is very evident from observation of the intact specimen (Fig. 8). Associated with the extreme reduction of M. pectoralis in *Atrichornis* is the loss of the distal part of the clavicular shaft (Figs 3, 5, 9). A similar phenomenon was reported in a few other species by Glenny & Friedmann (1954) who noted that the distal part of the clavicle sometimes remains as an unossified ligament (Ligamentum corpus claviculi). In *Atrichornis*, however, there was no sign of such a ligament, and the short clavicular shaft merely ended within the belly of the M. pectoralis (Fig. 3). In both forms, the sternal carina is correspondingly shallow.

Forelimb length. The lengths of the upper arm, forearm and manus were measured in the intact specimens after skinning; their sum is the total forelimb length. These values, divided by the cube root of body weight, give a measure of the lengths of the parts, relative to body size, corrected for differences in weight so that the species may be compared directly (Table 5). Compared to the reference species, *Atrichornis* shows about a 25% reduction in forelimb length. This reduction is not proportional in the three segments. Compared to the mean reference values, the upper arm is reduced about 5%, the forearm about 41% and the manus about 30%. The comparison with *Menura* is difficult because of the great difference in body size, but it is probably valid to assume that the relationship of wing length to body size holds across this range, as Greenewalt (1962) found this to be generally true with other wing length measurements across a much greater size range. Compared to the mean reference value, *Menura* shows a total forelimb length reduction of about 7%, with reduction in the individual segments being about 3% in the upper arm, 14% in the forearm and 5% in the manus. As in *Atrichornis*, the greatest reduction is in the forearm and the least in the upper arm. Although the values for *Menura* are below the means for the reference species, only the length of the forearm lies below the range of reference values. Thus, although *Menura* undoubtedly has a relatively short forelimb, it is uncertain to what extent this is biologically significant in relation to the reduction of flight. These values, though only rough estimates, do provide the means to compare the deviation of values in the Menurae from approximate expected values. In association with the nearly complete loss of the ability to fly, *Atrichornis* shows a clear reduction in forelimb length, and *Menura* a lesser but probably real reduction, both species having a similar pattern of relative reduction in the upper arm, forearm and manus.

Some brief comments on the reduction of flight in the Menurae, with additional specimen photographs, are presented elsewhere (Raikow, 1985: 85–86).

FUNCTIONAL ANATOMY OF THE HINDLIMB

Hindlimb length. The lengths of the thigh, crus and tarsus were measured, their sum being the total hindlimb length. As with the forelimb, these values were divided by the cube root of body weight to give comparative values. In this limb, both genera show relative elongation compared to the oscine 'standard' (Table 6). *Atrichornis* has a hindlimb 8.4% longer than the mean value, but not the highest value of the forms examined. *Menura* has a relatively longer hindlimb than any form examined (about 27% above the mean reference value). *Atrichornis* has its greatest elongation in the thigh (15% elongated), but less in the crus (8%) and tarsus (3%). *Menura* has less relative elongation in the thigh (6%), but a greatly elongated crus (32%) and tarsus (38%).

Fig. 8. Noisy Scrub-bird, *Atrichornis clamosus*, preserved specimen, photographed intact (above) and after skinning (below). Note the dorsoventral flattening of the body due to the greatly reduced pectoral muscles, and the relative proportions of the large hind limbs and reduced forelimbs.

Just as the forelimb shows reduction in length in the Menurae, the hindlimb shows relative elongation, especially in *Menura*. This is presumably correlated with these species' terrestrial habits, and probably also with the use of the legs for digging by *Menura*.

The preceding discussion has shown that the Menurae have rather short forelimbs and long hindlimbs. This is most clearly demonstrated by the ratio of total forelimb length to total hindlimb length (Table 6, last column). Despite differences in intramembral proportions, both genera are remarkably similar in this value, and distinctly separated from the other species studied.

Claws. In *Atrichornis* (Table 7), the claw of digit I is moderately longer than in the standard, while that of *Menura* is considerably longer. This may be related to their terrestrial habits, as an elongated first claw is not uncommon in passerines like longspurs and larks. However, in such cases this claw is usually rather straight, that is, having a small degree of curvature, which presumably helps to spread the bird's base of support on the ground. In the Menurae, however, the curvature is not drastically reduced (Table 9) and in the male *Menura* was quite high. Probably this is related to the use of the foot in grasping by *Menura*.

In *Atrichornis*, the claws of digits II, III and IV are relatively short and only moderately curved (Tables 7, 9), which is probably correlated with the fact that *Atrichornis* seldom, if ever, uses its feet either for perching or for grasping objects. Combined with the well developed claw of digit I, this gives the foot of *Atrichornis* a distinctive appearance (Fig. 10).

In *Menura*, the claws of digits II, III and IV are much elongated (Table 7), though not too sharply curved (Table 9). They are heavy and wide, and the tips are rounded off, perhaps by abrasion during digging. In typical passerines, the third digit is considerably longer than digits II and IV, and the same is true in *Atrichornis*. In *Menura*, however, these digits are almost as long as digit III. In addition, *Menura* is unique in that the claws

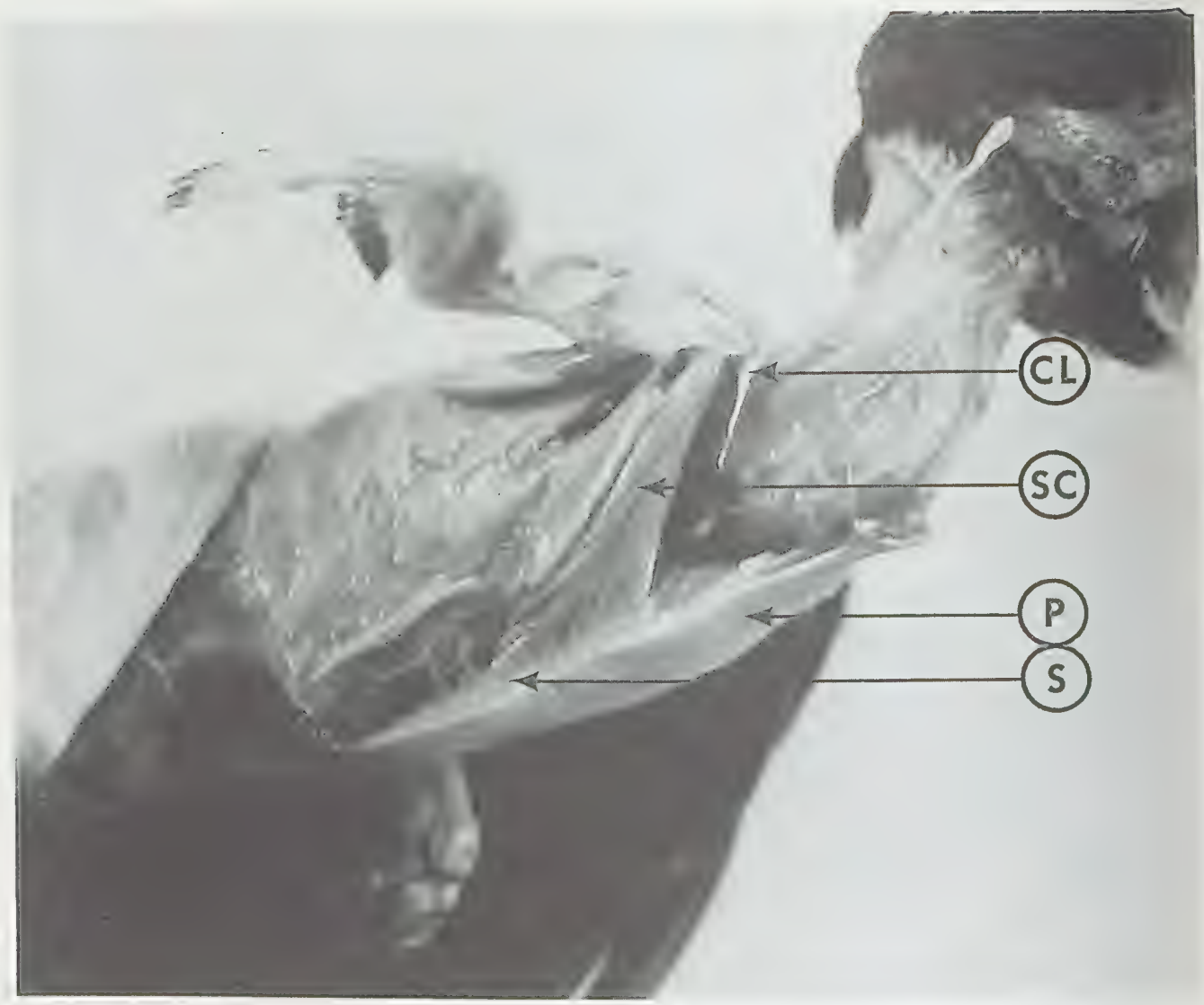

Fig. 9. Noisy Scrub-bird, *Atrichornis clamosus*, in ventrolateral aspect, following removal of the M. pectoralis on the right side of the body. Note the vestigial clavicle (CL) and the shallow sternal carina (S). Other abbreviations are as in Materials and Methods.

of digits II and IV are essentially equal in length to that of digit III, while in the other species, including *Atrichornis* (Fig. 10), they are shorter (Table 8). As a result, when the three anterior toes are held together the tips of the claws are nearly in line, rather than claw III extending beyond claws II and IV as is typical. This is perhaps an adaptation for digging, giving a cutting surface three times as wide as would otherwise be the case.

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Fig. 10. Foot of *Atrichornis clamosus* (left) and *Menura novaehollandiae* (right). Not to scale. Note that in the scrub-bird the claws of the anterior digits are relatively small and pointed, and that digit III extends well beyond digits II and IV. In *Menura*, however, the claws are extremely heavy, with rounded tips, and extend to nearly the same level. See text for discussion.

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Muscle	Menurae	Ptilonorhynchidae/Paradisaeidae
M. latissimus dorsi pars caudalis	Extremely enlarged with extensive area of origin	Narrow in usual passerine condition
M. pectoralis	Reduced in size	Normal size
M. supracoracoideus	Reduced in size	Normal size
M. tensor propatagialis pars brevis	Tendon of insertion fused with tendon of origin of M. extensor metacarpi radialis in *Menura*, separate in *Atrichornis*	Tendons separate in normal passerine manner
M. deltoideus major	Pars cranialis with proximal head	Proximal head lacking
M. deltoideus minor	Origin from apex of coracoid, slightly from scapula	Origin extensive from scapula alone in most Paradisaeidae, from coracoid and extensively from scapula in *Loria* and Ptilonorhynchidae
Forearm muscles	Relatively long	Relatively short

Table 1. Major differences in the forelimb muscles of the Menurae, the bowerbirds and the birds-of-paradise.

Muscle	Menurae	Ptilonorhynchidae/Paradisaeidae
M. iliofemoralis externus	Absent in both genera	Present in Ptilonorhynchidae and some Paradisaeidae
M. femorotibialis externus	More separate from M. femorotibialis medius	More fused to M. femorotibialis medius
M. femorotibialis internus	Single head and tendon	Two heads and tendons
M. flexor cruris lateralis	Origin from ilium only	Origin from ilium and caudal vertebrae
M. obturatorius lateralis pars dorsalis	Extremely small	Extremely large
	No origin from ventral edge of ilioischiatic fenestra	Originates from ventral edge of ilioischiatic fenestra
	Inserts on femur only	Inserts on femur and on tendon of M. obturatorius medialis
M. obturatorius medialis	Wider; doubly bipennate in medial aspect	Narrower; singly bipennate in medial aspect
M. iliofemoralis internus	Arises medial to M. iliotrochantericus medius	Arises caudal to M. iliotrochantericus medius
M. flexor perforans et perforatus digiti III	Bipennate for entire length	Bipennate proximally, unipennate distally
M. flexor perforatus digiti II	Tendon not bifurcate or perforated	Tendon bifurcate and perforated (most)
M. flexor hallucis longus	Origin of intermediate head fleshy	Origin tendinous
	Origin of medial head tendinous	Origin fleshy
M. flexor digitorum longus	Femoral head absent	Femoral head present in most Paradisaeidae
M. flexor hallucis brevis	Relatively small	Relatively large

Table 2. Major differences in the hindlimb muscles of the Menurae, the bowerbirds and the birds-of-paradise.

Muscle	*Menura*	*Atrichornis*
	FORELIMB	
M. pectoralis	Normal origin from clavicle	Origin from clavicle almost completely lost
M. supracoracoideus	Origin more extensive, including sternoclavicular membrane	Origin less extensive, not including sternoclavicular membrane
M. tensor propatagialis pars brevis	Tendon of insertion fused to M. extensor metacarpi radialis for entire length	Tendon of insertion separate except distally
M. deltoideus major	Proximal head of pars cranialis not distinctly separate	Proximal head distinctly separate
	HINDLIMB	
M. iliotibialis cranialis	Origin from median dorsal ridge of synsacrum and cranial edge of ilium	Origin from median dorsal ridge only
M. ischiofemoralis	Origin from lateral surface of ilium	Origin from lateral surface of ilium and caudolateral iliac crest
M. gastrocnemius	Patellar band wider	Patellar band narrower

Table 3. Major differences in the limb muscles of *Menura* and *Atrichornis*.

Species	Weight (g)	Percent-Weight of M. pectoralis	Percent-Weight of M. supracoracoideus
Menura novaehollandiae	921.4	5.64	0.64
Atrichornis clamosus	34.0	3.71	0.38
Zontrichia leucophrys	31.9	11.29	1.48
Chondestes grammacus	27.8	13.60	1.59
Carpodacus purpureus	30.0	14.80	1.27
Cardinalis cardinalis	40.0	12.05	1.38
Dumetella carolinensis	34.9	11.46	1.37
Mean of non-Menurae species		12.64	1.42

Table 4. Relative weights of the pectoral muscles.

Species	Upper Arm	Forearm	Manus	Total Forelimb Length
Menura novaehollandiae	7.31	6.61	6.53	20.45
Atrichornis clamosus	7.13	4.51	4.85	16.49
Zonotrichia leucophrys	7.03	6.72	6.06	19.81
Chondestes grammacus	7.52	7.92	7.33	22.77
Carpodacus purpureus	7.20	7.72	6.82	21.74
Cardinalis cardinalis	7.84	7.95	6.81	22.60
Dumetella carolinensis	7.95	7.98	7.37	23.30
Mean of non-Menurae species	7.51	7.66	6.88	22.04

Table 5. Forelimb measurements/cube root of weight.

Species	Thigh	Crus	Tarsus	Total Hindlimb Length	Forelimb length/ Hindlimb length
Menura novaehollandiae	6.80	14.65	8.86	30.31	0.67
Atrichornis clamosus	7.35	11.91	6.64	25.90	0.64
Zonotrichia leucophrys	6.78	11.29	6.69	24.76	0.80
Chondestes grammacus	6.01	10.36	6.11	22.48	1.01
Carpodacus purpureus	5.59	9.77	5.21	20.57	1.06
Cardinalis cardinalis	6.37	11.05	6.49	23.91	0.95
Dumetella carolinensis	7.31	12.84	7.61	27.76	0.84
Mean of non-Menurae species	6.41	11.06	6.42	23.90	0.92

Table 6. Hindlimb measurements/cube root of weight.

Species	Digit I	II	III	IV
Menura novaehollandiae (male)	3.26	2.52	2.50	2.44
Menura novaehollandiae (female)	3.06	2.57	2.45	2.32
Atrichornis clamosus	2.17	1.02	1.25	0.94
Zonotrichia leucophrys	2.04	1.18	1.46	1.09
Chondestes grammacus	1.56	0.92	1.31	0.97
Carpodacus purpureus	1.38	0.85	1.45	0.95
Cardinalis cardinalis	1.94	1.14	1.82	1.13
Dumetella carolinensis	2.07	1.27	1.83	1.25
Mean of non-Menurae species	1.80	1.07	1.57	1.08

Table 7. Claw length/cube root of weight.

Species	Digit II	Digit IV
Menura novaehollandiae (male)	1.00	0.98
Menura novaehollandiae (female)	1.09	0.98
Atrichornis clamosus	0.81	0.76
Zonotrichia leucophrys	0.80	0.76
Chondestes grammacus	0.72	0.74
Carpodacus purpureus	0.60	0.72
Cardinalis cardinalis	0.59	0.62
Dumetella carolinensis	0.71	0.71
Mean of non-Menurae species	0.68	0.71

Table 8. Lengths of claws II and IV/length of claw III.

Species	Digit I	II	III	IV
Menura novaehollandiae (male)	48.5	38.6	35.3	44.6
Menura novaehollandiae (female)	42.4	36.0	35.1	38.0
Atrichornis clamosus	41.5	34.4	37.8	37.5
Zonotrichia leucophrys	37.6	30.5	31.8	32.7
Chondestes grammacus	42.3	40.5	44.7	46.3
Carpodacus purpureus	51.2	42.6	42.7	42.3
Cardinalis cardinalis	45.9	46.1	45.0	43.4
Dumetella carolinensis	48.3	45.5	44.4	46.2
Mean of non-Menurae species	45.1	41.0	41.7	42.2

Table 9. Arcs of claws (degrees).

Muscles of the Neck, Trunk and Tail in the Noisy Scrub-bird, *Atrichornis clamosus*, and Superb Lyrebird, *Menura novaehollandiae* (Passeriformes: Atrichornithidae and Menuridae)

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Abstract. Muscles of the neck, trunk and tail of the Noisy Scrub-bird, *Atrichornis clamosus*, are described, illustrated and compared with those of the Superb Lyrebird, *Menura novaehollandiae*. It is proposed that hypertrophy of various neck muscles in *Atrichornis* is related to use of the head in penetrating litter and undergrowth. *Atrichornis* and *Menura* are shown to have qualitative differences in myology and in morphology of the uropygial glands, but taxonomic interpretation of these differences is judged to be premature without broader comparisons.

Zusi, R.L., 1985. Muscles of the neck, trunk and tail in the Noisy Scrub-bird, *Atrichornis clamosus*, and Superb Lyrebird, *Menura novaehollandiae* (Passeriformes: Atrichornithidae and Menuridae). Records of the Australian Museum 37(4): 229–242.

Keywords: myology, neck, trunk, tail, *Atrichornis*, *Menura*, Passeriformes.

The Noisy Scrub-bird, *Atrichornis clamosus* (Gould), is an endangered species of passerine bird restricted to Western Australia. The only other species in the genus, *Atrichornis rufescens* (Ramsay), occurs in eastern Australia. Until recently, little was known of the internal anatomy of either species, except for the structure of the syrinx, some peculiarities of the skeleton and notes on the myology of the shoulder (Fürbringer, 1888). In this paper I describe the skeletal myology of the neck, trunk and tail, from a single specimen of *Atrichornis clamosus* (adult female, Western Australian Museum A15926). Muscles of the tongue, jaws and appendages of that specimen have been described elsewhere (Bock, 1985; Raikow, 1985). In addition, I present comparative comments on the Superb Lyrebird, *Menura novaehollandiae* Latham, based on my dissection of a single specimen (adult female, Carnegie Museum Alc1834).

My primary purpose is to place the myological data from these specimens on record for comparison with other species. It is beyond the scope of this paper to make a critical appraisal of the phylogenetic relationships of *Atrichornis* because there is no existing body of data on these muscles for comparison. Such a study would require dissection of species from many oscine and suboscine families and subfamilies.

It is ironic that *Atrichornis* should be the subject of the first exposition of the trunk and tail muscles in a passerine bird since that of Shufeldt (1890) who described most of these muscles for the Common Raven, *Corvus corax* Linnaeus. Unfortunately his work is not always adequate for comparison with other species. Muscles of the trunk of the American Crow *Corvus brachyrhynchus* Brehm, were illustrated but not described by Hudson & Lanzillotti (1955). Several studies have dealt with passerine neck muscles: Shufeldt (1890) described the Common Raven (Corvidae); Palmgren (1949) compared a few species from the Paridae, Certhiidae, Sylviinae, Turdinae and Carduelinae; and Burton (1974) described the Callaeidae. Boas (1929) and Kuroda (1962) treated passerines only incidentally.

Palmgren (1949) interpreted most differences among the several families he dissected as adaptations for foraging. The differences are mainly in the relative sizes of muscles, in the numbers of slips of complicated muscles and in the vertebrae on which they attach. I have drawn tentative conclusions about the adaptations of *Atrichornis* based on limited comparisons of such differences.

MATERIALS AND METHODS

Dissection was done entirely under a dissecting

microscope and all drawings, except those labelled 'diagrammatic', were made by me in pencil with a camera lucida. No skeletal specimen of *Atrichornis* was available, and drawings of bony elements are therefore somewhat crude because of the presence of connective tissue or parts of muscles. The abdominal muscles had been cut and were shrunken and contorted, making camera lucida drawings impossible.

Terminology of muscles and bones generally follows that of Baumel *et al.* (1979). Myological differences between *Atrichornis clamosus* and *Menura novaehollandiae*, as well as some other passerines, are noted after the descriptions of *Atrichornis*, and when no difference is given, similarity between the two species is implied. Information on families other than Menuridae came from Palmgren (1949) and Burton (1974).

Throughout this paper the use of a numeral in a muscle description indicates a particular vertebra. Cervical vertebrae are numbered 1–14 beginning with the atlas, and the thoracic vertebrae, 15–19.

The following list identifies abbreviations that appear in the figures:

b c	M. (musculus) biventer cervicis
b r	M. bulbi rectricium
c	M. complexus
c a	M. cervicalis ascendens
cf	M. caudofemoralis
csp	M. costoseptalis
cst	M. costosternalis
cst ma	M. costosternalis, pars major
cst mi	M. costosternalis, pars minor
d c	M. depressor caudae
f c l	M. flexor colli lateralis
f c m	M. flexor colli medialis
ic	Mm. (musculi) intercristales
i e	Mm. intercostales externi
i i	Mm. intercostales interni
ilc	M. iliocostalis
in i	Mm. inclusi inferior
in s	Mm. inclusi superior
it	Mm. intertransversarii
la c	M. lateralis caudae
l c d ca	M. longus colli dorsalis, pars caudalis
l c d cr	M. longus colli dorsalis, pars cranialis
l c d p	M. longus colli dorsalis, pars profunda
l c d t	M. longus colli dorsalis, pars thoracica
l cl	M. levator cloacae
l co	Mm. levatores costarum
l c v	M. longus colli ventralis
l d d	M. latissimus dorsi dorsocutaneous
le c	M. levator caudae
o e a	M. obliquus externus abdominis
o i a	M. obliquus internus abdominis
p	Pygostylus
p e	M. pubocaudalis externus
p i	M. pubocaudalis internus
p s a	M. pectoralis, pars subcutanea abdominalis
r a	M. rectus abdominis
r c d	M. rectus capitis dorsalis
r c l	M. rectus capitis lateralis
r c v	M. rectus capitis ventralis
s	M. scalenus
s ca	M. splenius capitis
s cl	M. sphincter cloacae
se	M. serpihyoideus
t ab	M. transversus abdominis
t as	M. thoracicus ascendens
t c	M. transversus cloacae
u	Glandula uropygialis

OSTEOLOGY

Commonly used synonyms for some of the osteological terms in this paper are as follows:

This paper	Synonym
VERTEBRAE	
vertebral arch	neural arch
vertebral body	centrum
cranial articular process	prezygapophysis
caudal articular process	postzygapophysis
dorsal process	anapophysis
costal spine	cervical rib
costal process	'ansa' (Boas 1929)
carotid process	sublateral process
spinous process	neural spine
ventral process	hypapophysis
STERNUM	
trabecula lateralis	posterior lateral process
craniolateral process	sternocoracoidal process

The following comments are based on my observations on the skeletons of the spirit specimens of *Atrichornis clamosus* and *Menura novaehollandiae*, and skeletons of species from various other passerine families.

Both Palmgren (1949) and Burton (1974) stated that the neck in the passerine families they studied was subdivided into functional sections as follows: Section I, vertebrae 1–4; Section II, vertebrae 5–9; Section III, vertebrae 10–14 (Palmgren omitted the two cervical vertebrae that bear floating ribs from his count). My interpretation of the limits of Section II differs slightly from theirs. Boas (1929) defined the second section primarily on its capacity to bend upward, but not downward beyond a straight line. Nevertheless, he also included only vertebrae 5–8 or 5–9 in this section for various passerine families. I include vertebrae 5–10 in the second neck section of *Atrichornis*, *Menura* and the species studied by Palmgren and Boas, on the basis of the bending capability of that section and the associated morphology of the vertebrae. Vertebra 10 is intermediate in form between typical vertebrae of the second and third sections, but it more closely resembles the former. Thus, in my opinion, the neck sections of *Atrichornis* and *Menura*, as in many other passerines, are constituted as follows: I, 1–4; II, 5–10; III, 11–14.

Atrichornis and *Menura* have five free thoracic vertebrae and five ribs that attach on the sternum. Each

thoracic rib consists of a dorsal vertebral rib and a ventral sternal rib. In the sixth, or accessory rib, the vertebral rib articulates with the synsacrum and the associated sternal rib fails to reach the sternum. In addition, there are two floating cervical ribs — a small one from 13, and a larger one from 14 that bears an uncinate process. Spinous processes are borne on vertebrae 2–5, 6 (small), 13, 14 and the five thoracic vertebrae. Ventral processes occur on 2, 3, 4 and 10–15. Costal spines occur on vertebrae 3–12. The terms cranial, caudal, dorsal and ventral apply to the bird when its vertebral column is extended horizontally.

NECK MUSCLES

M. biventer cervicis (b c; Fig. 1A,B,C,D,E). This muscle consists of a long tendon interrupted by two fleshy bellies. The muscle lies superficial to M. longus colli dorsalis and partly deep to M. complexus. It originates from the spinous processes of 14, 15 and 16, and by an aponeurosis that is fused caudally with the underlying aponeurosis of M. longus colli dorsalis, pars caudalis. The aponeurosis of origin broadens as it passes craniad to the stout, strap-like caudal belly overlying vertebrae 13–18. From this belly, a broad tendon passes craniad through a connective tissue sheath enclosing the dorsal neck muscles over vertebrae 7, 8 and 9. The cranial belly begins at the level of 4 and ends on a short, broad aponeurosis that attaches on the occipital wall of the cranium between the insertions of M. complexus and M. splenius capitis.

In *Menura*, the muscle is proportionately weaker. It has tendons that are relatively more slender, thinner bellies and a shorter caudal belly covering only 12–10. It originates from 15.

M. complexus (c; Fig. 1A,B,C,D). This is a broad, flat muscle that lies superficially on the craniodorsolateral portion of the neck. The cranial portion of the belly is partially segmented by three tendinous intersections. Caudally, the belly is partially separated longitudinally into four major slips of origin. The most caudal arises by an aponeurosis, from the transverse process of 8, that fuses with an aponeurosis from 7 serving the second slip. The third slip arises from the lateral surface of the aponeurosis of origin of M. cervicalis ascendens, attaching on transverse process 6; the fourth slip arises similarly from 5. Fibres of these slips terminate on the caudalmost tendinous intersection. In addition, small slips arise from transverse processes 4 and 3, and terminate on the second tendinous intersection. The muscle inserts by fleshy fibres along a narrow line on the occipital wall of the cranium just dorsal to the insertions of M. biventer cervicis and M. splenius capitis. Laterally, the insertion is adjacent to the dorsal portion of M. rectus capitis lateralis.

In several passerine families, including Menuridae, this muscle arises only from 5 and 4 (small), or 6–5 (Certhiidae). *Heteralocha* has slips from 6, 5 and 4. This muscle is thus unusually well developed in *Atrichornis*.

M. splenius capitis (s ca; Figs 1A,B,C,D,E; 2A). This is a stout, fan-shaped muscle that lies deep to M. biventer cervicis, M. complexus and M. rectus capitis lateralis. It arises semitendinous from the tip of the spinous process of the axis, and fans out to its insertion. The insertion is along a narrow line on the occipital wall of the cranium, from the dorsal midline ventrally to the attachment of M. serpihyoideus (Fig. 1B) on the basitemporal plate. A small, flat slip arises separately from the tip of the dorsal process of the axis and joins the main belly at its ventrolateral area of insertion.

M. rectus capitis dorsalis (r c d; Fig. 1A,B,D,E). This muscle consists of two portions — a larger superficial part and a smaller deep part. The superficial part originates from the lateral surface of the vertebral arch of the atlas, the lateral edge of the axis ventral to the dorsal process, semitendinous from the dorsal process of 3, from a prominence on the lateral bar of 4, and by a narrow tendon from the craniolateral tip of the transverse process of 5. The third of these slips is the largest and the last very small. These slips partially coalesce as they converge cranioventrally on parallel tendons that form a bundle before inserting, along with fleshy fibres, on the basitemporal plate just medial to the cranial attachment of M. serpihyoideus.

The deep portion originates from the lateral edge of the vertebral arch of the axis, the lateral bar and the craniolateral surface of the transverse process of 3, and the prominence of the lateral bar of 4 deep to the attachment of the superficial slip. These slips converge on a short tendon that inserts on the basitemporal plate medial to the main insertion and just anterior to the lateral margin of the occipital condyle.

Menura is similar except that both the deep and superficial portions have their caudal attachment on 5. The caudal attachment in *Heteralocha* is from 5 or 6 (males), and in several other passerine families from 4.

M. rectus capitis lateralis (r c l; Fig. 1A,B,C,D,E). This is a superficial muscle of the craniolateral portion of the neck. It originates by flat tendons from the ventral processes of 3, 4 and 5, and by a slender tendon from the transverse process of 6 in company with M. rectus capitis ventralis. These tendons form a single, flat sheet that gives rise to the parallel fibres of the strap-like belly. The belly curves around those of M. longus colli ventralis and M. rectus capitis dorsalis to its insertion along the lateral portion of the occipital wall of the cranium lateral to M. splenius capitis. About midway along the line of insertion, fibres share the caudalmost portion of the aponeurosis of origin of M. depressor mandibulae. Ventrally, the insertion is deep to the hyoid horns and is semitendinous along the caudal edge of the attachment of the depressor mandibulae.

In *Menura*, this muscle arises by flat tendons from the ventral processes of 2–5; in *Parus*, 4–6; *Certhia*, 3–5; *Pyrrhula* and *Phoenicurus*, 1–4; and *Heteralocha*, 2–4.

M. rectus capitis ventralis (r c v; Figs 1A,E; 2C). This muscle lies on the cranioventral surface of the neck, medial to M. rectus capitis lateralis. It originates fleshy

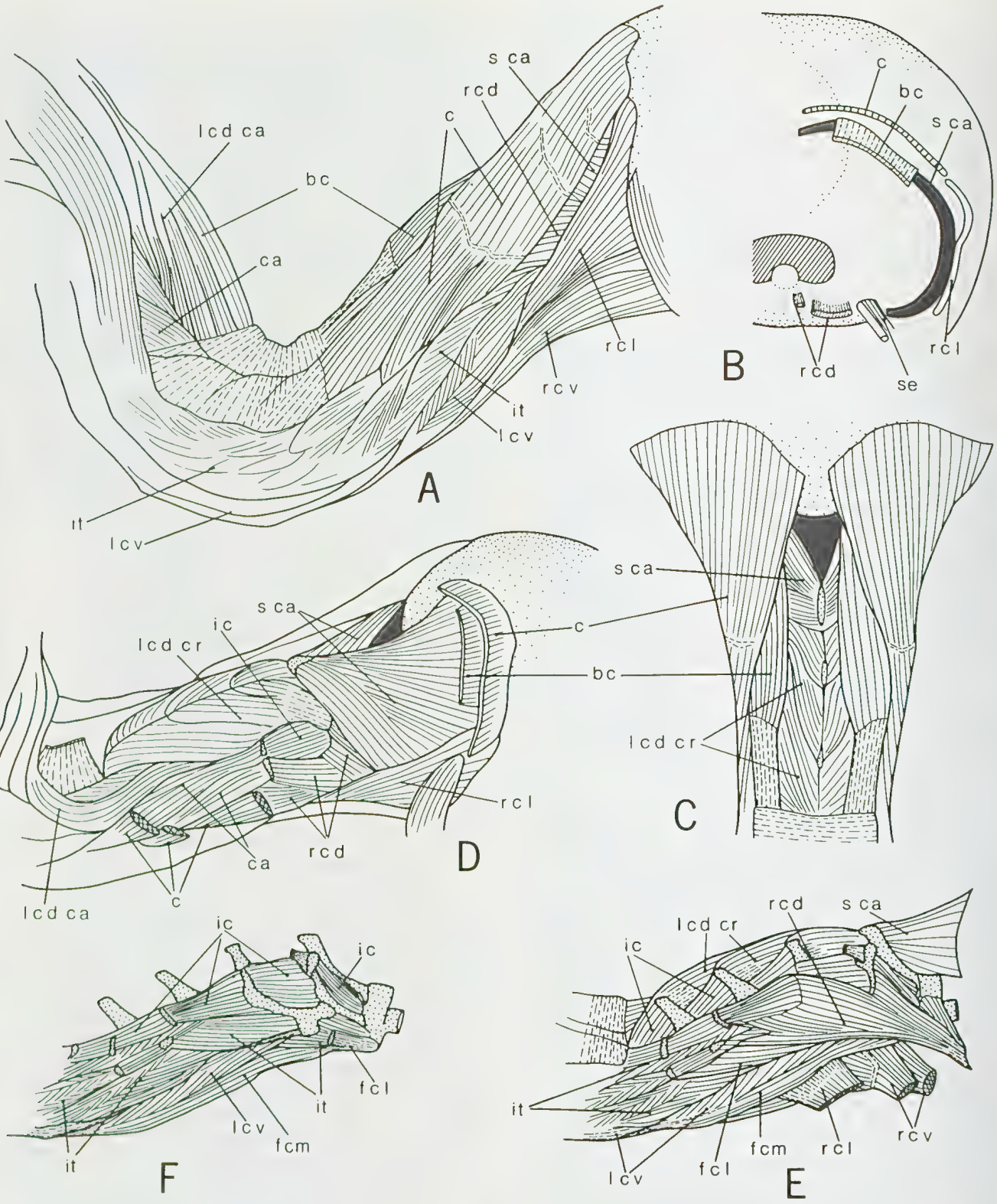

Fig. 1. Neck muscles of *Atrichornis clamosus*. **A**, superficial muscles, right side. **B**, insertions on occipital surface of skull (diagrammatic). **C**, dorsal view of anterior muscles. **D**, dorsolateral view of anterior muscles; M. complexus and M. biventer cervicis removed. **E**, lateral view of second layer of anterior muscles, right side; M. rectus capitis lateralis and M. rectus capitis ventralis cut and reflected. **F**, lateral view of deep anterior muscles. Abbreviations see Materials and Methods.

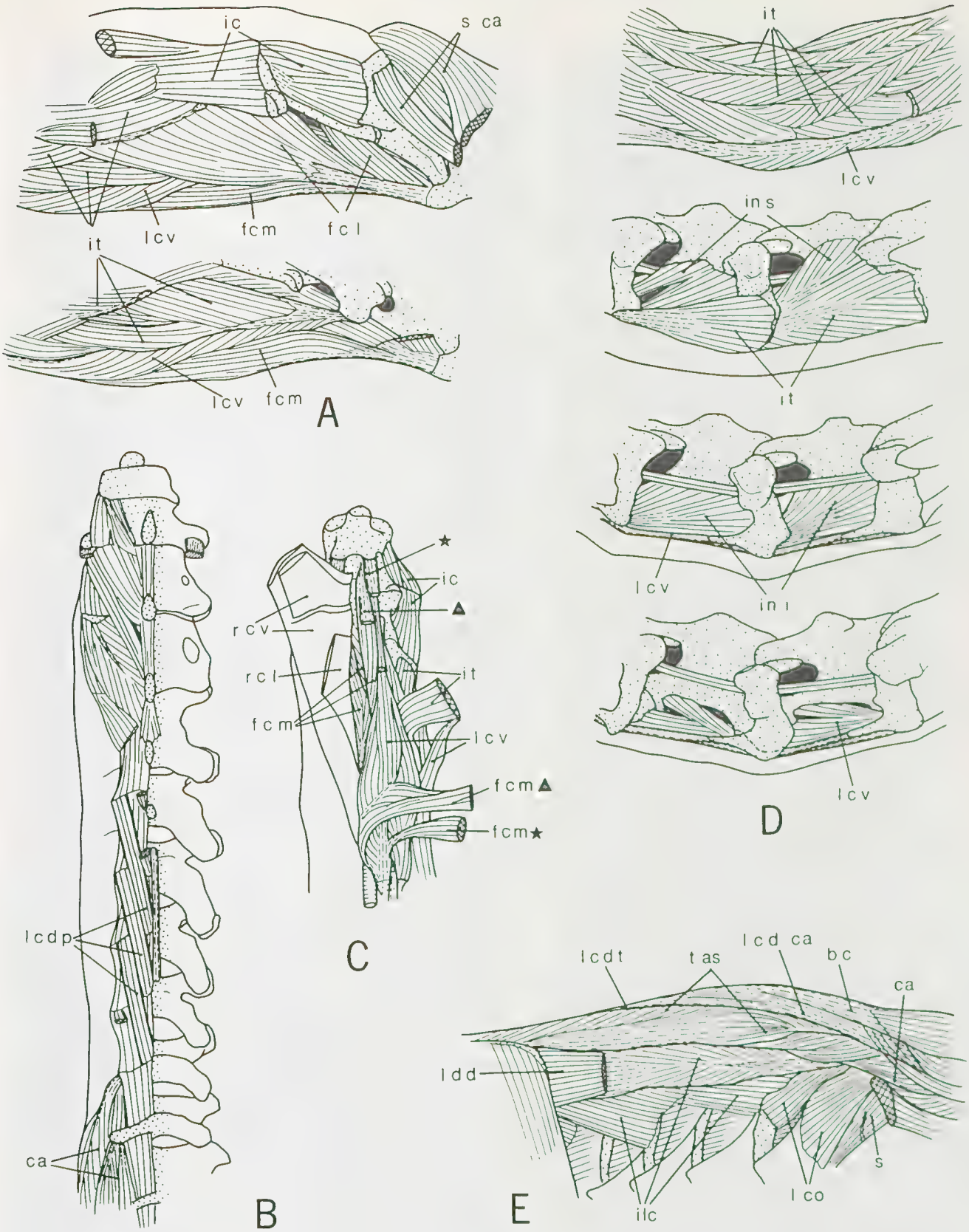

Fig. 2. Neck and trunk muscles of *Atrichornis clamosus*. **A**, lateral views of deep anterior muscles, right side; above, M. rectus capitis dorsalis removed; below, M. flexor colli lateralis removed. **B**, dorsal view (all unlabelled muscles are Mm. intercristales). **C**, ventral view of deep anterior muscles; M. rectus capitis ventralis and M. rectus capitis lateralis cut and reflected to opposite side. **D**, lateral musculature of vertebrae 7 and 8, right side. Top to bottom shows superficial to deep layers. Outline of l c v deep to costal process shown by dashed line in bottom figure. **E**, lateral view of dorsal trunk muscles, right side. Abbreviations see Materials and Methods. Stars and triangles identify different bisected portions of M. flexor colli medialis.

from the ventromedial surfaces of vertebrae 2, 3, 4 and 5, and by short, flat tendons from the ventral processes of those vertebrae. The caudalmost slip arises by a short tendon from the transverse process of 6, just lateral to the carotid artery. A separate dorsal slip of this muscle arises from the ventral process of 2 and from a narrow aponeurosis. This aponeurosis passes laterally and joins an intersection that crosses the dorsal surface of the main belly. Insertion of the entire muscle is fleshy on the basitemporal plate of the cranium, anterior to the insertions of M. rectus capitis dorsalis.

The caudal limit of this muscle differs within passerines: vertebra 4 in *Carduelis* and *Phoenicurus*; 5 in *Pyrrhula* and *Regulus*; 6 in *Menura*, *Parus*, *Acrocephalus* and *Heteralocha*; and 7 in *Certhia*. None of these genera exhibits the extra slip from 2 found in *Atrichornis*.

M. cervicalis ascendens (c a: Figs 1A,D; 2B,E). This muscle consists of a series of overlapping bellies lying along the dorsolateral portion of the neck. Each belly contains several slips that originate from the transverse processes of two or more vertebrae and pass cranially to converge on a common insertion on the dorsal process of a single vertebra. Bellies inserting on 5, 6 and 7 have two slips each, a slender one from the second vertebra caudal to that of insertion, and a larger one from the third vertebra caudal to that of insertion. The larger slip inserts on the medial side of an aponeurosis that is shared by the smaller slip and by a slip of M. longus colli dorsalis. Bellies inserting on 8–12 have three, and sometimes four, slips of origin. The additional slips arise from successively more caudal vertebrae and are typically weak. The belly to 13 has two slips. Its insertion on the caudal articular process is deep to the tendon of insertion of the first slip of M. thoracicus ascendens. The bellies inserting on the dorsal processes of 3 and 4 also have three slips each, originating from 5, 6, 7, and 6, 7, 8, respectively.

In *Menura*, this muscle differs in having only two slips of origin for the cranial five bellies as follows: 3(insertion)–6,7(origins); 4–6,7; 5–7,8; 6–8,9; 7–9,10.

M. longus colli dorsalis, pars cranialis (l c d cr; Fig. 1C,D,E). This muscle consists of five stout slips arising from the dorsal surface of the vertebral arch of 6 and 7, and from the lateral and cranial surfaces of the spinous processes of 3, 4 and 5. These slips insert sequentially on the medial, dorsal and ventral surfaces of the tendon of insertion of pars caudalis, attaching on the dorsal process of the axis. The fleshy belly of pars caudalis of this muscle attaches on this tendon between the fourth and fifth slips of pars cranialis.

Menura is similar. Origins of slips in some other forms are: 6–4, *Acrocephalus*; 7–4, *Parus*; 6–4 or 7–4, *Heteralocha*; 9–4 (not 8), *Pyrrhula*.

M. longus colli dorsalis, pars caudalis (l c d ca; Figs 1A,D; 2E). This is the major dorsal muscle of the neck, acting in opposition to M. longus colli ventralis. It consists of a series of overlapping, flattened slips that insert on the dorsal process of the axis and on 6–13. The slip to the axis is the largest and its insertion is by a stout tendon that also serves as insertion for pars cranialis. Attachments on 6–13 are semitendinous, each sharing an aponeurosis of insertion with a belly of M. ascendens cervicis. The slips arise in succession from the ventral surface of a common aponeurosis that extends forward and fans out from the tips of the spinous processes of 14 through 18. The origins of slips 1, 4 and 5 attach across the full breadth of the aponeurosis of origin, 2 and 3 only on the lateral portion, 6 and 7 on the medial portion, and 8 and 9 on all but the medialmost part. Origins of these slips occupy the aponeurosis from the level of 12–15.

Menura differs in that the origins of all slips occupy almost the full breadth of the aponeurosis that originates from 14–17. The insertions to 6–9 are by tendons that are buried in the inserting slips of M. cervicis ascendens. A separate insertion by short tendon attaching medial to the dorsal process is present on 8 and 9. Insertions on 10–14 are broad and fleshy on the transverse-oblique crest.

M. longus colli dorsalis, pars profunda (l c d p; Fig. 2B). This muscle is largely confined to the second neck section. It consists of a series of strap-like bellies that extend from the midline of the vertebral arch of one vertebra to the dorsal process of the second vertebra cranial to it. On the left side I found only three bellies (8 to 6, 9 to 7, 10 to 8), all with fleshy attachments on both ends, whereas on the right side two additional bellies connected vertebrae 11 and 9, and 12 and 10. The caudal attachment of each of these additional bellies was by a short, flat tendon.

Menura has three developed bellies (8 to 6, 9 to 7 and 10 to 8). *Heteralocha* has four or five — the first between 8 and 6, and the last between 11 and 9 or 12 and 11. Some passerines have two bellies, some only one and others none.

Mm. intercristales (ic; Figs 1D,E,F; 2A,B,C). These muscles include the Mm. interspinales and Mm. splenii accessorii of other authors. The interspinales portion consists of those fibres that interconnect successive spinous processes: 2–3, 3–4, 4–5, 12–13, 13–14, 14–15.

Most of these muscles are flat bellies connecting successive vertebrae at their transverse-oblique crests and dorsal processes. They lie deep to M. longus colli dorsalis profundus and caudalis, and medial to Mm. ascendens cervicis. Bellies of this description begin at 13–12 and end at 6–5, and are broadest at 10–9, 9–8, 8–7. The insertion on 5 is atypical, attaching at the base of the spinous process and on a prominence craniolateral to it.

In neck section I these muscles abruptly become larger and more complex. In addition to the interspinales, bellies between 5 and 4, 4 and 3, 3 and 2, and 2 and 1 consist of a lateral portion from one dorsal process to the next, and a dorsal portion passing craniolaterally from the lateral surface of the spinous process (this portion not present between 5 and 4) and

the dorsal surface of the vertebral arch to the adjacent vertebra. Three additional slips lie superficially and pass from the base of the spinous process to the dorsal process as follows: 5 to 3, 4 to 2, 2 to 1. The caudal slip arises semitendinously and inserts, in part, on an aponeurosis from the dorsal process that also receives fibres from the vertebral arch of 4. The middle slip is entirely fleshy, whereas the cranial slip arises semitendinously and inserts by a slender tendon.

Menura is similar except for the pattern of superficial slips just described. I found only two slips, both fleshy, as follows: 5 to 3, 4 to 3.

Mm. intertransversarii (it; Figs 1A,E,F; 2A,C,D). These bellies interconnect the transverse processes and costal processes of successive vertebrae. The caudalmost belly originates from 13 and the cranialmost inserts on the axis. Bellies from 10 through 6 are similar in structure. Laterally, they consist of interdigitating aponeuroses from origin and insertion with short fibres arranged in multipennate fashion. Deep to this portion, a stout aponeurosis passes forward from its origin on the ventral portion of the costal process and gives rise to fibres that fan out and insert on the ventrolateral and caudal surfaces of the adjacent costal process. Dorsal to this portion lies M. inclusi superior and deep to it, M. inclusi inferior. Cranial to vertebra 6 this series becomes simplified and reduced to two major slips in each belly. One joins successive transverse processes and the other passes forward from the costal process to the medial surface of the adjacent costal spine, costal process and vertebral body. Only a single slip is present between 3 and the ventrolateral surface of 2. The belly of the main series of this muscle between 11 and 12 is reduced to a dorsal and a ventral slip, and that between 12 and 13 to a single dorsal slip.

In the first neck section, an additional series of slips passes craniad from the costal process to the tip of the costal spine as follows: a stout slip from costal process 5 and a cylindrical slip from 7 attach on an aponeurosis to costal spine 3; a stout slip from 6 and a slender one from 7 attach on an aponeurosis to costal spine 4; a fleshy slip extends from the costal process of 6 to the lateral surface of costal spine 5. The aponeuroses of insertion of the slips to costal spines 3 and 4 are fused ventrally with the aponeuroses of insertion of M. longus colli ventralis.

Menura is similar but I found that the tendon to costal spine 3 received fibres from costal processes 4, 5 and 6, and that to 4 received a few fibres from 6.

Mm. inclusi (in; Fig. 2D). This series of bellies extends craniad from the craniomedial surface of the costal process to the lateral surface of the body of the adjacent vertebra. Most bellies are divided into a superior and an inferior slip, separated longitudinally by the vertebral artery. The superior slip (in s) inserts on the lateral surface of the vertebral arch, and the inferior slip (in i) on the lateral surface of the vertebral body. Both slips arise from the medial surface of a fan-shaped aponeurosis whose lateral surface is occupied by fibres of Mm. intertransversarii. The inclusi are thus closely associated with those muscles, and the cranial and caudal bellies are scarcely separable from them. The most cranial of the typical bellies connects 6 and 5; superior slips are lacking between 5 and 4, and 4 and 3. Caudally, the last complete belly is between 12 and 11; the last belly (13 to 12) contains only the inferior slip.

In *Menura*, the first small belly lies between 4 and 5, and consists of only the inferior slip. The last two bellies (10 to 11, 11 to 12) also contain only the inferior slip. The five intervening bellies are two-parted and typical.

M. longus colli ventralis (l c v; Figs 1A,E,F; 2A,C,D). This is the major ventral muscle of the neck, acting in opposition to M. longus colli dorsalis. It consists of a series of parallel overlapping bellies originating from the carotid processes or ventral processes, and inserting by tendons on the tips of the costal spines. These bellies inserting on the first neck section originate from 7; all others originate from the third neck section and first thoracic vertebra.

The cranial bellies insert on the ventral portions of aponeuroses shared by Mm. intertransversarii and attaching as short tendons on the costal spines of 3 and 4. Most of the ventral portion of the tendon or origin of these cranial bellies serves as origin for parts of M. flexor colli medialis.

The first and ventralmost of the long bellies to neck section II inserts by a flat tendon on costal spine 5. A series of fleshy slips arising from the carotid processes, ventral surfaces of the vertebral bodies, and the ventral processes of vertebrae 8–12 joins the long aponeurosis of this belly. Each of the bellies inserting on successive vertebrae (6–12) receives a slip from the vertebral body of the adjacent vertebra, and slips from the ventral processes or carotid processes of all succeeding vertebrae. The belly to 6 extends caudally as far as ventral process 14; those to 7–11 extend back to a common aponeurosis arising from ventral process 15. A belly from 12 originates on 13 and 14.

In the pattern of bellies and slips of *Menura*, the belly inserting on 5 originates from 7–11; those to 6 through 12 all extend back to 15. *Menura* lacks a slip from the body of the vertebra adjacent to that of insertion, as found in all but the first of the long slips of *Atrichornis*. Space occupied by that slip in *Atrichornis* is taken by the intertransversarii and inclusi muscles in *Menura*. The belly to 4 receives slips from 6 and 7.

M. flexor colli lateralis (f c l; Figs 1E,F; 2A). This is a fan-shaped muscle of the anterior portion of the neck, lying mostly deep to M. rectus capitis dorsalis. It originates from the lateral surface of the costal spine of 3, the cranial articular process and the edge of the lateral bar of 4 caudally to its prominence, from the costal processes of 5 and 6, and from an aponeurosis shared by the intertransversarii between those vertebrae. The fibres converge onto the dorsal surface of a tendon that inserts on the ventral process of the atlas. This tendon is shared by a belly of M. flexor colli medialis.

In *Heteralocha* (females), *Menura* and *Regulus* the origin is from 3, 4 and 5. An additional slip from 6 is present in males of *Heteralocha*.

M. flexor colli medialis (f c m; Figs 1E,F; 2A,C). This is the deepest muscle of the cranioventral portion of the neck. It consists of a series of cylindrical slips that interconnect the vertebrae of the cranial half of the neck. The cranialmost slip is stout and cylindrical. It originates from the lateral surface of a flat aponeurosis from the carotid process of 7 that is shared by the cranialmost slip of M. longus colli ventralis. It inserts by a stout tendon on the ventral process of the atlas. Two slips insert by an aponeurosis on the ventral process of the axis — a major slip from the medial portion of the aponeurosis from 7, and a stout slip from the lateral surface of an aponeurosis from the ventromedial portion of transverse process 5. The ventral portion of the vertebral body of 3 receives fleshy fibres from the medial surface of an aponeurosis from 5 and from an aponeurosis arising on the carotid process of 6. Similarly, the centra of 4 and 5 receive fibres from the carotid processes of 5 and 6, and 6 and 7, respectively.

In *Menura* I found slips from the carotid processes of 7, 6 and 5 to the ventral process of the axis. From 6, slips also go to 3 and 4. In *Heteralocha* and some other oscines the insertions are on 2, 3 and 4.

TRUNK MUSCLES

Muscles of the trunk vertebrae are complicated, interconnected and not always clearly related to the neck muscles. Their nomenclature also is confusing. In birds, the name 'M. longissimus dorsi' has been applied to different portions of the vertebral musculature of the thorax (compare Shufeldt, 1890, and Vanden Berge, 1975). Consequently, I shall not use the term 'longissimus dorsi', but instead describe all the muscles of the thoracic vertebrae under the names M. iliocostalis, M. thoracicus ascendens and M. longus colli dorsalis, pars thoracica. I tentatively regard these muscles as continuations and elaborations of Mm. intertransversarii, M. cervicalis ascendens and M. longus colli dorsalis, pars caudalis, respectively. Development of a more meaningful terminology for these muscles must await further comparative studies within birds, and between birds and reptiles.

M. longus colli dorsalis, pars thoracica (l c d t; Fig. 2E). This muscle constitutes the medialmost portion of the muscle mass that occupies the trough formed by the transverse processes and the spinous processes of the thoracic vertebrae. The slips of this muscle interconnect the spinous processes, and also extend from spinous processes to the caudal articular processes of the thoracic vertebrae.

There are two sets of aponeuroses of origin and two sets for insertion. Superficially, the long, narrow aponeuroses of origin of M. longus colli dorsalis, pars caudalis, send a few muscle fibres cranioventrad to a series of strong, underlying aponeuroses of insertion that extend caudolaterally from the dorsocaudal tips of the spinous processes of 14–18. Most of the lateral surface of these aponeuroses is occupied by fibres of M. thoracicus ascendens. Zusi & Bentz (1984) referred these aponeuroses to M. thoracicus ascendens, but I prefer now to follow Boas (1929) in treating them as part of M. longus colli dorsalis, pars thoracica, because of their intimate relation to its aponeuroses of origin. Deep to these aponeuroses of insertion, another set of flattened aponeuroses of origin extends cranioventrolaterally from the dorsocranial edge of the spinous processes of 17–19 and from the cranial edge of the fused synsacral spinous processes. Fibres from the lateral surface of these aponeuroses insert on the medial surface of the aponeuroses of insertion described above, and fleshy and by aponeuroses on the caudal articular processes of 13, 14 and the thoracic vertebrae. Fibres from their medial surface insert fleshy on the spinous processes and vertebral arches of the first or second vertebrae cranial to that of origin; fibres to aponeuroses from the spinous processes insert on the third, fourth and fifth vertebrae cranial to that of origin.

In *Menura*, the aponeuroses of origin of the deep part of the muscle attach on spinous processes 16 (small), 17, 18 and 19.

M. thoracicus ascendens (t as; Fig. 2E). This muscle constitutes a major portion of the musculature of the thoracic vertebrae. It lies between M. longus colli dorsalis, pars thoracica and M. iliocostalis, and shares aponeuroses with both. The limits of these three muscles are clear only at their origins and insertions.

The superficial fibres of this muscle originate from both walls of the synsacral trough, and from the ventral and ventromedial surfaces of a long, partially superficial aponeurosis that extends craniad over most of the muscle from the craniodorsal edge of the ilium. The lateral surface of the deep portion of this aponeurosis is occupied by M. iliocostalis. The fibres of the superficial portion of M. thoracicus ascendens are compacted and only partially separable into slips. The more dorsal fibres insert on the almost continuous surface formed by the series of flat aponeuroses of insertion from the caudal tips of the spinous processes of 14–18 described under M. longus colli dorsalis, pars thoracica.

The deeper fibres of this muscle arise from the medial surface of the aponeurosis shared by M. iliocostalis, and from the transverse processes and their aponeuroses (described under M. iliocostalis). The fibres extend craniomedially to the aponeuroses from the caudal articular processes of 13, 14, and of the thoracic vertebrae which they share with M. longus colli dorsalis, pars thoracica.

M. iliocostalis (ilc; Figs 2E, 3A). This is the lateralmost of the thoracic muscles of the vertebral column. It lies lateral to M. thoracicus ascendens and dorsal to the dorsomedial portion of the thoracic ribs. The origin consists of a series of long, flattened, parallel and overlapping aponeuroses from the craniolateral tips

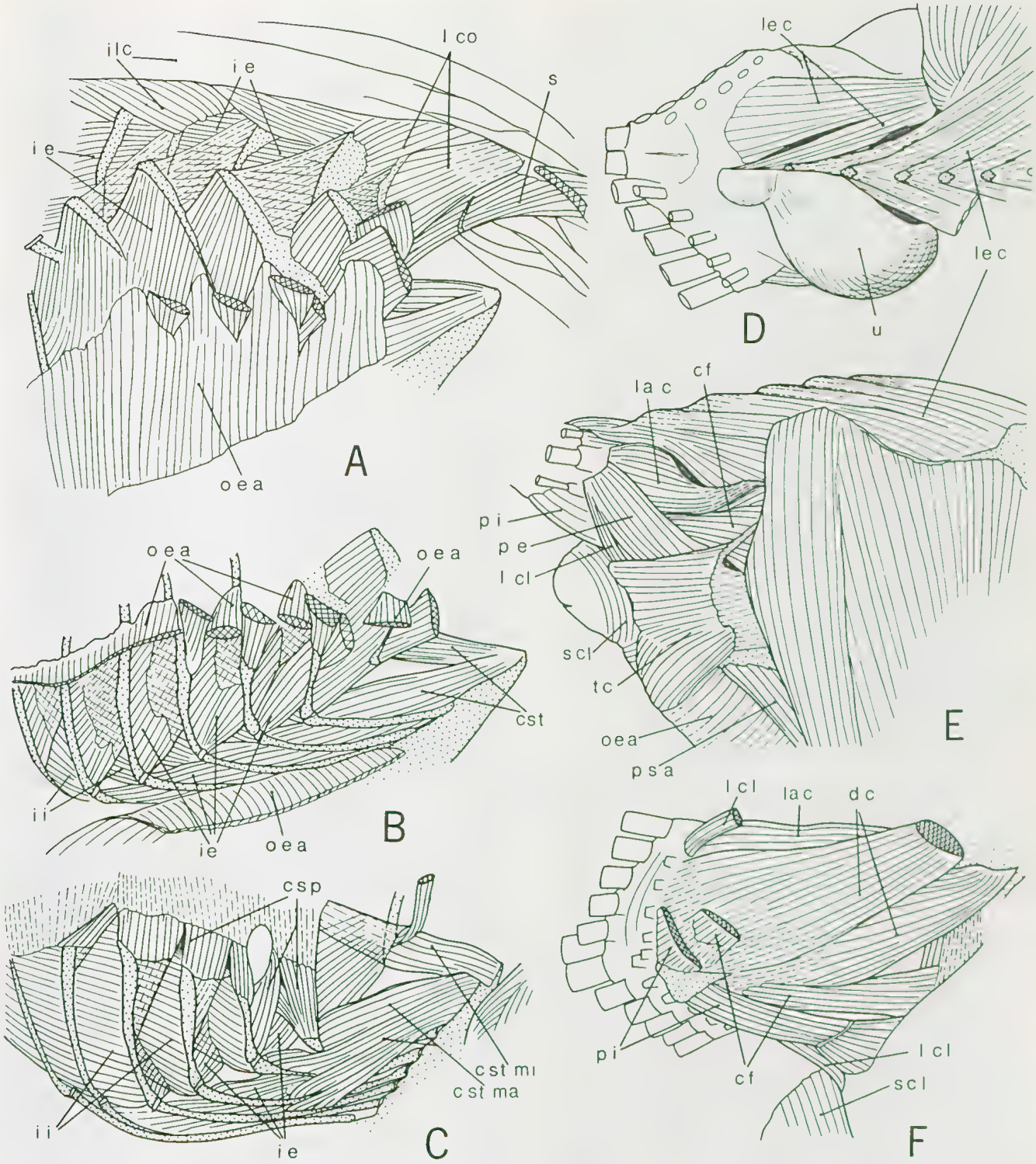

Fig. 3. Trunk and tail muscles of *Atrichornis clamosus*. **A**, superficial muscles of thorax, right side (cut muscles are serratus group). **B**, right lateral view of lower rib cage (M. obliquus externus abdominis cut and reflected). **C**, medial surface of lower left thoracic wall. **D**, dorsal view of tail; left uropygial gland removed. **E**, superficial muscles of the tail and abdomen, right side. **F**, ventrolateral surface of tail muscles, right side; M. pubocaudalis externus removed; cloaca reflected downward toward left side. Abbreviations see Materials and Methods.

of transverse processes 19–16, and from the cranial edge of the ilium. These aponeuroses are largest caudally. In the caudal half of the muscle, an additional large area of origin is from the lateral surface of a long aponeurosis from the ilium shared by M. thoracicus ascendens. Insertion is on a series of overlapping aponeuroses attaching on the caudolateral tips of the transverse processes of 13–18. These aponeuroses pass caudolaterally and cross those of origin dorsally. Fibres converge on the tendons of insertion in pennate fashion, and the bulk of the muscle inserts on the tendons to 13 and 14.

The lateralmost fibres of this muscle originate from the ventral portion of the long aponeurosis from the cranioventral edge of the ilium, and from the aponeuroses of origin from 19–16. These fibres pass craniolaterally to insert fleshy on the dorsolateral surfaces of the thoracic ribs.The cranialmost fibres to the first attached rib have a separate origin from rib 3.

That this muscle may be a thoracic continuation of Mm. intertransversarii is suggested by its interconnections with transverse processes of the thoracic vertebrae, and the close association of its major insertion on 13 with the caudalmost belly of the intertransversarii. Its attachments on the thoracic ribs may be homologous with those of the intertransversarii on the costal spines in the first neck section.

In *Menura*, the slips attaching on the ribs also attach on aponeurotic sheets extending back from their dorsocaudal edges. The slip to the first rib inserts by a narrow, flat tendon. These slips, except for the caudalmost, are mostly deep to the main belly.

Mm. levatores costarum (l co; Figs 2E, 3A). This series of muscles connects the transverse processes with the thoracic ribs and the second floating rib. All but the two cranial bellies lie deep to the lateral portion of M. iliocostalis. The cranialmost levator is the largest. It arises from the ventrolateral surface of the transverse process of 13, and from a superficial aponeurosis. Fibres fan out caudoventrally to insert on the lateral and cranial surfaces of the uncinate aponeurosis, and on an adjoining aponeurosis. The three caudal bellies originate by an aponeurotic sheet from the ventral edge of the preacetabular wing of the ilium and insert on the 4th, 5th and 6th (accessory) thoracic ribs. Each insertion is on a flattened depression of the thoracic rib from the tuberculum, laterally to the ventral curvature of the rib. The insertion is aponeurotic distally and lies between the intercostales externi and interni muscles.

In *Menura*, the first belly (from 13) is less developed than that of *Atrichornis*, inserting only on the upper lateral surface of the second floating rib. The third belly is largely superficial rather than covered by a slip of M. iliocostalis.

M. scalenus (s; Figs 2E, 3A). This muscle is probably serially homologous with the levatores costarum. It arises fleshy from the ventrolateral surface of the transverse process of 12, and inserts on the entire cranial and lateral surfaces of the first floating rib.

Mm. intercostales externi (i e; Fig. 3A,B,C). These muscles consist of a series of flat bellies interconnecting successive thoracic ribs and floating ribs. Each muscle of the thoracic ribs has three separate portions — two associated only with the vertebral ribs and one only with the sternal ribs. I shall call these the vertebral portion, the uncinate portion and the sternal portion.

The vertebral portion is a thin sheet of fibres extending from one rib to the next, from the lateral surface of the iliocostalis muscle to the attachment of the uncinate process. The fibres attach on the opposing edges of the two ribs and, to varying degrees, on their lateral surfaces. The fibres pass mainly cranially, but somewhat dorsally as well, from the caudal to the cranial attachment. The cranialmost of these bellies connects the two floating ribs.

The uncinate portion is a thin sheet connecting the cranial half of each uncinate process with the entire process cranial to it. Ventral to the uncinate process, the sheet connects adjacent ribs ventrad as far as their articulations with the sternal ribs. The uncinate portion lies superficial to the vertebral portion where they overlap. Fibres are oriented dorsally or craniodorsally from their caudal attachment to the next rib. Ventral to the uncinate process, the fibres extend only about half way to the more cranial rib; there they give way to a thin aponeurotic sheet, with the following exceptions: fibres extend from one rib to the other ventrally between thoracic ribs 3 and 2, 2 and 1, and between 1 and the second floating rib.

From the craniodorsdal edge of each uncinate process, an aponeurosis (uncinate aponeurosis) extends craniodorsally to the caudal edge of its rib. This aponeurosis stabilizes the uncinate process against the pull of the uncinate portion of this muscle.

The sternal portion is thicker than the other portions and it passes between successive sternal ribs (1 and 2, 2 and 3, and 3 and 4). The muscles become smaller caudally and the connection between 4 and 5 is largely aponeurotic, containing only a few short fibres dorsally.

Mm. intercostales interni (i i; Fig. 3B,C). This is a series of thin sheets of muscle interconnecting successive thoracic vertebral ribs. The muscles lie deep to the intercostales externi and pass cranioventrally from the edge of one rib to the edge of the adjacent rib. The cranialmost belly connects the first and second floating ribs; the caudalmost connects the fifth thoracic and sixth (accessory) ribs. Fleshy fibres connect successive ribs only in the ventral portions of the three caudal bellies; elsewhere the fibres are restricted to the cranial half of the muscle and attach caudally on an aponeurotic sheet.

M. costosternalis (cst; Fig. 3B,C). Pars major (cst ma) of this muscle extends from the caudal and lateral surfaces of the craniolateral process of the sternum to the ventral end of the first thoracic vertebral rib and to all the attached sternal ribs, deep to M. intercostalis externus. The sternal attachment is both fleshy and by a superficial ventral aponeurosis, whereas costal attachments are mainly fleshy. The slips become

progressively smaller caudally, with that to the fifth rib attaching only by a slender aponeurosis.

Pars minor (cst mi) is a stout slip that attaches fleshy on the tip of the craniolateral process of the sternum and passes dorsocaudally where it is bound to the tip of the second floating rib. It continues onto its insertion on the cranial edge of the first attached rib by a flat aponeurosis.

Pars minor in *Menura* has no binding to the second floating rib and it passes directly to a fleshy attachment on the first attached rib.

M. costoseptalis (csp; Fig. 3C). This is a series of muscle sheets inside the thoracic cavity that connect the lateral portion of the horizontal septum with the vertebral portions of the five attached ribs. Attachments on the first two ribs are fleshy; those on ribs 3, 4 and 5 partly fleshy and partly aoneurotic. The muscles lie deep to the intercostales interni.

M. obliquus externus abdominis (o e a; Fig. 3A,B,E). This is an extensive sheet of muscle covering the ventral portion of the rib cage and the abdomen. It originates fleshy from the ventral angles of the uncinate processes of the first floating rib and first three thoracic ribs, and by an aponeurotic sheet from the fifth and sixth uncinate processes. Cranially, the uncinate attachments interdigitate with the costal attachments of M. serratus superficialis. The sheet also attaches fleshy on the lateral surfaces of the third and fourth thoracic ribs, and by an aponeurotic sheet on the fifth and sixth (accessory) ribs. The line of origin of this muscle sheet continues caudally across an aponeurosis covering the dorsolateral abdominal wall to the ventral edge of the pubis. Fibres originate along the edge of the pubis as far as its distal tip.

The sternal insertion is by a short, broad aponeurosis attaching along the entire lateral border of the trabecula lateralis of the sternum. The abdominal insertion is on the linea alba. This muscle is crossed superficially by M. pectoralis subcutaneous abdominis.

M. rectus abdominis (r a; Fig. 4). This sheet of muscle passes from the caudal edge of the sternum to the distal portion of the pubis and the linea alba. The long lateral fibres pass primarily caudad to the pubis, but those from more medial portions of the sternal border become progressively shorter as their direction becomes more medial. The muscle is superficial to the ventral portion of M. obliquus internus and to much of M. transversus abdominis, and is covered laterally by M. obliquus externus abdominis.

M. obliquus internus abdominis (o i a; Fig. 4). This is a flat sheet of fibres extending between the last thoracic rib and the proximal half of the pubis. The dorsal border of the muscle is aponeurotic and curves to accommodate passage of blood vessels to the thigh.

M. transversus abdominis (t ab; Fig. 4). This muscle passes mainly transversely from the cranial edge of the distal portion of the pubis to the linea alba. Craniodorsally its attachment on the pubis is by an

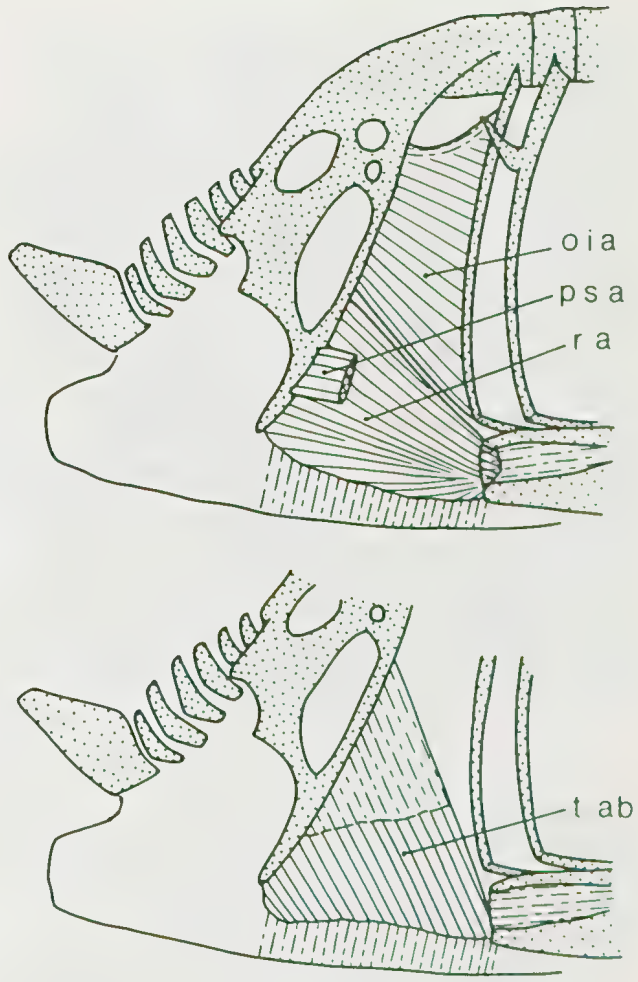

Fig. 4. Abdominal muscles of *Atrichornis clamosus*. Right side; diagrammatic. Above, M. obliquus externus abdominis removed. Below, M. obliquus internus abdominis and M. rectus abdominis removed. Abbreviations see Materials and Methods.

aponeurotic sheet. Its dorsolateral fibres are overlapped by the ventral portion of M. obliquus internus abdominis.

M. transversus cloacae (t c; Fig. 3E) This muscle lies largely superficially on the caudolateral surface of the trunk. It arises by an aponeurotic sheet from the caudal edge of the terminal process of the ischium and the adjacent dorsal edge of the pubis. Its origin parallels and is lateral to that of M. pubocaudalis internus and is separated from it by the belly of M. pubocaudalis externus. Additional origin is by a narrow aponeurosis from the terminal process of the ilium and the tip of the transverse process of the third free caudal vertebra. This aponeurosis extends caudoventrally to meet the dorsal edge of the main aponeurosis, thus forming a loop that is penetrated by M. caudofemoralis. Fleshy fibres arise from the entire conjoined aponeurosis, caudal to the loop, and form a sheet that attaches on the surface of the sphincter cloacae and on the linea alba caudal to the limit of M. transversus abdominis.

M. sphincter cloacae (s cl; Fig. 3E,F). This is a broad band of muscle that encircles the cloaca just

cranial to the vent.

This muscle was not available for comparison in *Menura* because the cloaca had been removed from the specimen.

M. levator cloacae (l cl; Fig. 3E,F). This is a slender band of muscle that arises from the caudoventrolateral corner of the retricial bulb, medial to the attachment of M. pubocaudalis externus. It passes ventrally to insert on the dorsolateral wall of the cloaca, cranial to M. sphincter cloacae and medial to the dorsal attachment of M. transversus cloacae.

The muscle was not available for comparison in *Menura*.

M. pectoralis, pars subcutanea abdominalis (p s a; Figs 3E, 4). This strap-like, fleshy muscle originates from the cranial border of the distal portion of the pubis and passes forward, superficial to M. obliquus externus abdominis, to insert on the inner surface of the lateral skin of the breast.

In *Menura* the muscle originates as a flat aponeurosis from the distal portion of the pubis. Fleshy fibres begin at about the level of the caudal end of the rib cage and continue onto the skin of the breast.

TAIL MUSCLES

Baumel (1971) pointed out that rectrices of the pigeon (*Columba livia* Gmelin) have little direct fibrous attachment to the tail skeleton, and that all but the central pair are implanted into a fibro-adipose mass that he called the 'retricial bulb'. This structure articulates in a shiny connective tissue socket supported by the tail skeleton and musculature (see also Vanden Berge, 1975:1813). In *Atrichornis*, all retrices are included in the bulb, but the central pair is closely bound by connective tissue to the caudal portion of the pygostyle; cranially the bulb has a looser connective tissue connection with the pygostyle. Thus, motions of the tail are effected by muscular action on the free caudal vertebrae and pygostyle, on the right and left retricial bulbs, and on the individual feathers within the bulb.

M. levator caudae (le c; Fig. 3D,E). This muscle is partially separable into dorsal and ventral portions. The dorsal portion consists of a series of parallel and contiguous slips that originate from the entire dorsal surface of the postacetabular wing of the ilium, the adjacent surface of the fused synsacral vertebrae and the vertebral arches of the free caudal vertebrae. These slips pass caudomedially to insert fleshy, and by superficial aponeuroses, on the tips of the dorsal processes of the free caudal vertebrae. The ventral portion lies deep to the uropygial gland (Fig. 3D). It originates fleshy from the dorsal surfaces of the transverse processes of the free caudal ventebrae and fans out to insert on the tendinous surface of the rectrical bulb.

In *Menura* the dorsal fibres of insertion of the ventral portion of this muscle attach on the aponeurotic cranial surface of the uropygial gland. Unlike those of *Atrichornis* (see Fig. 3D), the two glands are fused cranially, forming a continuous surface across the caudal vertebrae.

M. lateralis caudae (la c; Fig. 3E,F). This muscle is largely superficial on the lateral surface of the tail musculature. Ventrally, its fibres are scarcely separable from those of the depressor caudae. It originates from the tips of the transverse processes of free caudal vertebrae 3–6. The fibres fan out over the surface of the rectricial bulb where they insert deep to M. levator caudae. The major bulk of the belly arises from 3 and 4, and attaches on the lateral edge of the retricial bulb between the levator and the depressor caudae.

M. depressor caudae (d c; Fig. 3F). This is the major ventral muscle of the tail. It arises from the caudal edge of the fused synsacral vertebrae and from the ventral surfaces of the transverse processes of the free caudal vertebrae. The fibres pass caudoventrally to insert on the tips of the ventral processes of the free caudal vertebrae and on aponeuroses that extend cranially from them. A major part of the insertion is on an extensive superficial aponeurosis that attaches on the ventral edges of the pygostyle, whereas the more caudolateral fibres insert on that portion of the aponeurosis that attaches on the rectricial bulb and the bases of the caudal retrices. Aponeuroses passing caudally from the caudal edges of the transverse processes of the ultimate and penultimate free caudal vertebrae, send fibres in pennate fashion to the ventrolateral surface of the pygostyle.

M. pubocaudalis externus (p e; Fig. 3E). This lateral muscle of the tail lies superficial to M. transversus cloacae caudally, and deep to it cranially. The strap-like belly originates from the caudodorsal edge of the pubis and passes dorsally to its insertion on the caudolateral corner of the rectricial bulb and the base of the lateral rectrix.

In *Menura*, this muscle is broader at its insertion, meeting the lateral edge of pubocaudalis internus about halfway across the retricial bulb.

M. pubocaudalis internus (p i; Fig. 3E,F). This muscle lies mainly deep to M. pubocaudalis externus. It originates from the caudal edge of the terminal process of the ischium and the adjacent dorsal edge of the pubis. The pubic origin is immediately deep to that of pubocaudalis externus but it extends less far caudally. The muscle passes dorsocaudally to its insertion on the superficial aponeurosis of M. depressor caudae along the caudolateral edge of the pygostyle, and laterally along the bases of all but the lateral two major undertail coverts. A tendinous, transverse intersection divides the belly into a shorter cranial portion and a longer caudal portion.

In *Menura*, this muscle meets the medial edge of pubocaudalis externus about half way across the retricial bulb.

M. caudofemoralis (cf; Fig. 3E,F). This is a large muscle that originates on the femur, passes caudally through a loop in the aponeurosis of M. transversus

cloacae, and continues caudally, ventral to M. lateralis caudae and deep to the two pubocaudalis muscles. Its insertion is on the superficial aponeurosis of M. depressor caudae cranial to (and deep to) the insertion of M. pubocaudalis internus. Through that aponeurosis its force is directed to the ventrolateral edge of the pygostyle.

The caudofemoralis of *Menura* inserts by a rounded tendon. The tendon fuses with that of the opposite caudofemoralis muscle to form a single median tendon that attaches on the caudoventral surface of the pygostyle. This common tendon separates the right and left pubocaudalis internus muscles.

M. bulbi rectricium (b r; Fig. 5). This muscle consists of a series of stout slips on the ventral side of the rectricial bulb deep to M. depressor caudae. The slips originate in sequence from the aponeurotic cranioventral surface of the bulb and pass caudomedially to aponeurotic attachments on the under tail coverts and on the rectrices between the stout tendons of insertion of M. depressor caudae. A slip supplies each of the retrices except the lateral one in each rectricial bulb. The medialmost slip also includes fibres from the craniomedial surface of the bulb that converge on a tendinous sheet attaching on the medial surface of the follicle of the inner rectrix and on the adjacent caudal surface of the pygostyle. The lateral rectrix receives fibres on the dorsal, lateral and ventral surfaces of the base of its follicle from a muscular sheet that curves around the craniolateral corner of the bulb from its origin on the aponeurotic dorsal surface of the bulb. This slip is deep to M. lateralis caudae. A small sheet of fibres from the centrolateral surface of the bulb passes over the cranial edge to the dorsolateral surface. Most of the dorsal surface of the bulb is aponeurotic.

In *Menura*, this muscle is somewhat more complex. Its description is not included here as it might better accompany a detailed study of the rectricial bulb in relation to the use of the tail for display.

I did not find M. adductor retricium in *Atrichornis*.

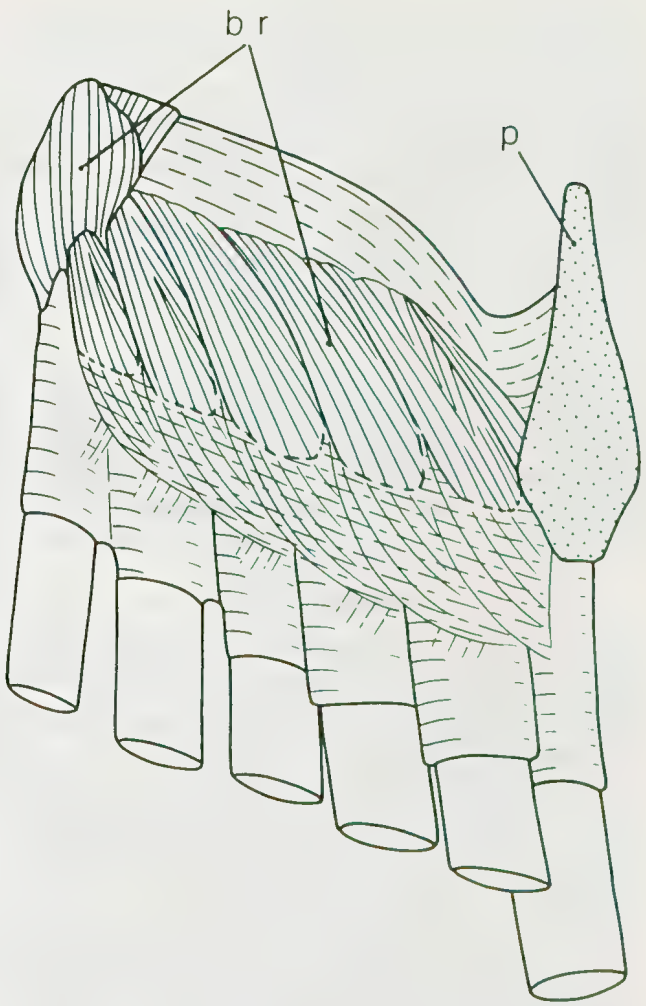

Fig. 5. M. bulbi retricium of *Atrichornis clamosus*. Ventral view of retricial bulb, right side. M. depressor caudae and M. lateralis caudae removed. Abbreviations see Materials and Methods.

DISCUSSION

Individual variation in avian muscles, even of different sides of the same bird, is of common occurrence. Comparisons drawn between species from single specimens must thus be made with caution because differences may have no taxonomic or adaptive significance. Variations in the number of slips of a muscle or in the vertebrae on which they attach are particularly frequent. Nevertheless, the occurrence of additional slips or relatively larger muscles or stouter tendons in seven muscles of the anterior portion of the neck of *Atrichornis*, when compared to *Menura*, strongly suggests an adaptation for unusually forceful movements of the head, and neck section I, in *Atrichornis clamosus* (see Mm. biventer cervicis, complexus, cervicalis ascendens (cranial part), longus colli dorsalis profundus, flexor colli lateralis, flexor colli medialis, rectus capitis ventralis). A basis for these modifications is suggested by an account of the habits of *Atrichornis rufescens* that appeared in Mathews (1919–1920:27). Speaking of birds foraging on the ground in undergrowth, he quoted Ramsay's comment that "They moved by a series of short hops, putting their heads under the loose, dead leaves and forcing themselves along in such a manner that the leaves passed over their backs, so that at times they were completely hidden, and could only be detected by the slight movement of the leaves over them." Of *A. clamosus*, Smith (1976) stated that "It spends most of its time feeding on the ground. It searches for food by poking its head under the litter, or flicking leaves aside with the bill. The feet are not used" (p. 130). Use of the head and neck as a 'ploughshare' in litter and dense vegetation, and use of the bill rather than the feet for clearing the ground could account for hypertrophy of the neck muscles. Unfortunately, because of the extreme difficulty of seeing scrub-birds, there is no detailed account of the use of the bill in foraging.

Several qualitative differences between *Atrichornis* and *Menura* may have taxonomic significance. These

are the presence of an extra slip and tendinous intersection of M. rectus capitis ventralis in *Atrichornis*, the presence of a slip to the centrum of the vertebra adjacent to that of insertion in bellies of the longus colli ventralis of *Atrichornis*, the different configurations of the uropygial gland and their relation to M. levator caudae in the two genera, and the differences in the insertion of M. caudofemoralis. The taxonomic significance of these differences cannot be properly evaluated without broader comparison of these and other features.

ACKNOWLEDGEMENTS. I am indebted to Mary Clench for her efforts in obtaining the specimens of *Atrichornis clamosus* and *Menura novaehollandiae*. Mary Rowland translated portions of Palmgren (1949), and Carolyn Cox Lyons skilfully rendered all of the original pencilled drawings in ink.

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Morphology of the Noisy Scrub-bird, *Atrichornis clamosus* (Passeriformes: Atrichornithidae): Systematic Relationships and Summary

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ABSTRACT. Evidence provided in this monograph supports the conclusion that the genera *Atrichornis* and *Menura* are sufficiently distinct for each to be placed in a monotypic family, viz. the Atrichornithidae and the Menuridae. The suborder Menurae, in which these two families are usually placed, should be merged with the suborder Oscines of the Passeriformes as the differences between them are not sufficiently large to justify continued recognition of these two suborders. The Atrichornithidae and the Menuridae are each other's closest relatives, but the evidence available in this monograph does not suggest an especially close relationship to the Ptilonorhynchidae. It is recommended that the Atrichornithidae and the Menuridae be placed in a superfamily, the Menuroidea, of unknown affinities within the Oscines. The Menuroidea do not appear to be primitive within the Oscines. They are not closely related phylogenetically to the Rhinocryptidae of the Tyranni. Reduction in flying ability of the Menuroidea is presumably advanced in the Oscines and is reflected in a number of morphological features of the skeletomuscular system. The extreme terrestrial habits of the species of the Menuroidea, together with the long incubation and fledgling periods of the single annual chick (two in *A. rufescens*), may be contributing to their decline. Moreover, the scrub-birds and lyrebirds may be relict remnants of an earlier larger radiation, and are unable to compete successfully with other avian species and/or to cope with recent changes in the environment, such as the introduction of foxes and feral cats. Conservation efforts for the scrub-birds and lyrebirds should consider the morphological and systematic findings presented in this monograph in addition to ecological data, with the suggestion that the undertakings for the Two Peoples Bay population of *Atrichornis clamosus* serve as a model for future actions.

BOCK, WALTER J. & MARY HEIMERDINGER CLENCH, 1985. Morphology of the Noisy Scrub-bird, *Atrichornis clamosus* (Passeriformes: Atrichornithidae): systematic relationships and summary. Records of the Australian Museum 37(4): 243–254.

KEYWORDS: Menuroidea, Menuridae, Atrichornithidae, Noisy Scrub-bird, systematics, morphology.

In the concluding paper to this monograph on *Atrichornis clamosus*, we would like to cover several points that are general to all of the individual contributed studies, as well as to provide an overview of the major findings. In particular, we wish to present a full discussion, including an historical summary, of the systematic relationships of the Atrichornithidae and of the suborder Menurae in which they have usually been placed. This analysis must include, of course, the Menuridae. We emphasize at the onset that the views expressed herein are our own and do not represent a consensus of the authors of the individual contributions. We do not wish to supercede these individual opinions, but we will use freely the evidence presented in the several papers, although we may sometimes reach different conclusions.

Three technical points must be made about the results of studies based on the 'Upper Coffin' specimen of

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Atrichornis clamosus which formed the foundation of this monograph. The bony stapes was sent to Alan Feduccia. He chose not to present his results with the other authors in this monograph, but published his ideas separately (see Feduccia & Olson, 1982). The syrinx was sent to Peter Ames. Upon dissecting it, he found that its morphology corresponded to that described earlier in his monograph on the passeriform syrinx (Ames, 1971:86–87) and felt that an additional description was not justified. Ames kindly provided an informal report to the organizers of this project for which we express our appreciation. Blood and other tissues were taken in Australia and sent separately to Professor Charles G. Sibley of Yale University to use in his comparative studies of DNA–DNA hybridization of birds. Because of the schedule of Professor Sibley's research program it would not have been possible for him to provide a contribution to this monograph. He has, however, kindly made available to us manuscripts of his findings (Sibley & Ahlquist, 1985, in press) and has given us permission to use this information for our summary.

Summary of the Monograph and Associated Studies

The first three papers deal with the plumage. Using the flat skin technique, Clench (1985) provided a detailed description of the body pterylosis of *Atrichornis* and *Menura*, and compared it with the pterylosis of a large number of Australasian and other birds suggested as possible relatives of the Menurae. She found that *Atrichornis* and *Menura* have extremely dense feathering, both dorsally and ventrally. The pattern of feathering, however, showed no close similarity to that of any other group of passerines. Using the clipping method, Morlion (1985) described the pterylosis of the wing and tail of these two genera, but was unable to undertake any further comparative analysis. She reported that *Menura* has 11 primaries and 14 secondaries. The wing and tail feathers of *Atrichornis* are not greatly different from those of other passerine birds. Smith (1985) described the natal downs and the feather development in wild and captive chicks of *Atrichornis clamosus*. Chicks have a dense line of grey down from the crown to the rump, with small thin patches on the shoulders and thighs. Fledglings have a plumage similar to that of the female but with bright rufous patches on the forehead, chin and throat. These bright patches may provide easier location by the female of her young lurking in dark vegetation.

Rich, McEvey & Baird (1985) described and compared the postcranial skeleton of both species of *Atrichornis* and the two species of *Menura*, but were unable to carry out a detailed comparison with other groups that might be allied to these genera. They discussed those osteological features cited by Feduccia and Olson (1982) as being similar in the Menurae and in the Rhinocryptidae, and alluded to by these authors as suggesting a close relationship between the groups. Rich *et al.* (1985) argued that a number of these features were found in other terrestrial passerines and suggested that the similarities in the Menurae and the Rhinocryptidae were the result of convergent adaptation for terrestrial life.

Bock (1985) described the skeletomuscular system of the jaw and tongue apparatus in *Atrichornis clamosus* and made some comparisons with the skull of *Menura*. Both genera possess a large, free lacrymal — largest in *Menura*. No special features were found in the jaw muscles of *Atrichornis*, but this bird has five features of its tongue musculature and one of its tongue skeleton which are advanced for passerine birds, and one feature of the tongue musculature which may be primitive. These attributes of the tongue suggest that the Atrichornithidae may not be primitive among the passerine birds, as is usually believed.

In a short preliminary report to the monograph authors, Feduccia showed that *Atrichornis* has a stapes similar to that seen in the Oscines. In a separate paper, Feduccia & Olson (1982) argued that *Atrichornis* and *Menura* share many osteological similarities with the Rhinocryptidae of South America, and hinted at a relationship between these groups.

Raikow (1985) described the appendicular myology of *Atrichornis* and *Menura* and, based on his work and that of his students, compared it with the myology of many other passerine groups. He discussed, in detail, modifications seen in these two families that are associated with the reduction of flight and with increased terrestrial locomotion.

Zusi (1985) described the trunk and axial muscles, including those of the tail, in *Atrichornis* and *Menura*. As he stated, it is ironic that the first study of the trunk and tail muscles for a passerine bird since that of Shufeldt (1890) should be for an endangered species. Zusi was unable to make comparisons with other passerine birds. *Atrichornis* has strongly developed cervical muscles, compared with those of *Menura*. Zusi suggested that the larger size of these muscles may be associated with the use of the head, by *Atrichornis*, to clear leaf litter when feeding.

Ames reported (in litt) that his study of the syrinx from the 'Upper Coffin' specimen simply confirmed the information gained from the earlier (c. 1889) specimen on which he had already published (1971:86–87).

Sibley & Ahlquist (1985, in press) compared *Atrichornis* with *Menura* and a large number of other passerine birds in their extensive survey of DNA–DNA hybridization in birds. They argued that these comparisons show that *Atrichornis* and *Menura* are sister groups and are most closely related to the Ptilonorhynchidae within the corvine complex.

The result of the studies in this monograph is that we now have an excellent knowledge of the morphology of *Atrichornis clamosus*, as good as that for any other passerine bird — and better than for most. A problem does exist in that only one specimen was available for dissection and hence nothing is known about individual variation. But this is true for most anatomical studies of avian species. Except in the case where they were

already engaged in a broad-based, comparative-systematic analysis (Clench; Raikow; Sibley & Ahlquist), the authors were unable to undertake a comparison of their findings from *Atrichornis* with those from passerine birds other than *Menura*. This situation resulted from the fact that several authors interrupted their research program to take part in this cooperative venture, and were unable to conduct an extensive comparative study at the time. Thus, we are left with a detailed knowledge of *Atrichornis* and *Menura*, but lack information on other passerine groups to permit those comparative analyses necessary for detailed taxonomic conclusions. As repeatedly expressed by the authors of the individual papers, a broad-based, detailed survey of these morphological systems is needed, especially for Australasian and other relevant passerine families. We believe, however, that the present monograph permits a few conclusions and we hope it will stimulate further work in this area.

Taxonomic Relationships of *Atrichornis* and *Menura*

Historical survey. The taxonomic position of *Atrichornis* and *Menura* has attracted the attention of ornithologists ever since these birds were discovered. *Menura* was believed to be a gallinaceous bird when it was first described (e.g. Vigors, 1825:486–7). Chisholm (1951) has reviewed the taxonomic history of *Atrichornis*, and Sibley (1974) that of *Menura*. Because of a number of errors and differences in interpretations, and the need to bring the literature review up to date, we will present a historical overview of the systematics of these birds. To avoid confusion between similarly appearing, but actually different conclusions, we took pains to check all original sources cited herein. Although *Atrichornis* is the subject of this monograph, a discussion of its taxonomic history is not possible without that of *Menura*. Unless otherwise stated, our comments refer equally to *Atrichornis* and *Menura* — the Menurae.

Although Vieillot (1816:12–13,48) had earlier suggested that *Menura* is a passerine bird, Nitzsch (1840; see 1867:82–83) was the first ornithologist to provide solid morphological evidence supporting placement of this bird in the Passeres. Contrary to Sibley (1974:66), Nitzsch did not ally *Menura* with the Clamatores, the New World non-oscines, but placed it in a group "Subulirostres *seu* Canorae" which included most of the insect-eating oscines as well as a few non-oscines such as *Pteroptochos*. In his monograph, Nitzsch did not have a concept of oscine versus non-oscine passerines. When *Atrichornis* was discovered, it was thought to be related to genera such as *Dasyornis* (the bristlebirds), *Psophodes* (the whipbirds) and *Orthonyx* (the logrunners or chowchillas); all reasonable suggestions (Chisholm, 1951). Relationship of *Menura* to the Rhinocryptidae (the tapaculos of the Neotropics) was suggested by Eyton (1841:52; **not** Eyton, 1841, Notes on Birds, No. II (sic), Ann. Mag. Nat. Hist. 7:177–179 as cited by Ames, 1971:165 and followed by Sibley, 1974:78 — this paper deals with *Biziura lobata*!). Eyton's conclusions on the possible relationships of *Menura* are difficult to unravel. He stated (1841:52) that it may belong to the Pteroptochidae (= Rhinocryptidae) or perhaps to the Megapodiidae (Galliformes); quite different conclusions. Cabanis (1847:201–202, 337) concluded that *Menura* cannot belong to the songbirds because of its large number of wing and tail feathers and placed it as a subfamily Menurinae in the Eriodoridae (Clamatores). Cabanis's family Eriodoridae included mainly the Formicariidae, but also the Pittidae, the Rhinocryptidae and the former Conopophagidae. Contrary to Sibley (1974:66), Cabanis did not follow Nitzsch and did not place *Menura* in the Pteroptochidae. Later, Sclater (1874:191) said "there seems to be no doubt that the *Menura* represents a distinct family, 'Menuridae', quite different from all other Passeres, and to be referred to the division Oscines", but in a footnote he suggested that *Atrichornis* may be a member of the Pteroptochidae (= Rhinocryptidae) on the mistaken information that its sternum has two emarginations on each side of the posterior border. In recent years, Feduccia & Olson (1982) have resurrected the idea of a close relationship between the Menurae and the Rhinocryptidae.

Müller (1847:330) did not dissect the syrinx of *Menura* in his monograph on the syringeal muscles of passerine birds, but relied on the description of Eyton (1841). He stated that *Menura* possesses the oscine type of syrinx (Müller, 1847:367) and discussed similarities between the lyrebird and the larks. Müller placed (p. 384) the Menuridae between the Certhiidae at the end of the oscine series and the Myiotheridae (= Formicariidae) at the beginning of the tracheophone series. In his final remarks (p. 385) Müller stated that *Menura* has an oscine syrinx and implied that he believed it is allied to the songbirds. Unfortunately, Müller hedged on his ideas on the affinities of *Menura*, probably because he was unable to dissect its syrinx himself.

Wallace (1874:413) placed the Menuridae in the formicarioid Passeres (non-oscines) based strictly on the structure of the 10th primary (= his 1st primary). He did not realize that *Menura* has 11 primaries (see Morlion, 1985). Wallace argued that the Menuridae are closely related to the Pteroptochidae (= Rhinocryptidae). He did not mention *Atrichornis*.

Newton (1896:524) claimed to be the first ornithologist, in 1875, to suggest a close affinity between *Atrichornis* and *Menura*. His statement (Newton, 1875:741) in the section on 'Geographic distribution of birds' in his article 'Birds' is: "Australia, however, possesses two extraordinary families of abnormal *Passeres* — the Lyre-birds (*Menuridae*) and the Scrub-birds (*Atrichiidae*) — which, so far as is at present known, stand by themselves, though it is possible that the latter have a somewhat distant ally in the genus *Orthonyx* or even in the South American family *Pteroptochidae* [= Rhinocryptidae]." Although

suggestive, this statement is too vague to be considered a sufficient claim of close relationship between *Menura* and *Atrichornis*. Newton (1875) could not have adopted Garrod's classification for these birds, which was first published in 1876, contrary to Sibley's statement (1974:66). Much confusion also exists on the citation to Newton's two major articles on birds in the famous 9th edition of the Encyclopedia Britannica (see Sibley, 1974:79). These articles are not both 'Ornithology', in two different editions — the 9th in 1875 and the 18th in 1885 (not 1884 as cited by Sibley). Rather they are on 'Birds', in volume 3 in 1875 and on 'Ornithology', in volume 18 in 1885, both in the 9th edition of this encyclopedia. The second article (Newton, 1885), updated, was used by Newton as the introduction to his 'Dictionary of Birds' (1896).

The first conclusion with strong morphological support for a close relationship between *Atrichornis* and *Menura* was that of Garrod (1876). He argued on the basis of a number of features — the M. tensor patagii brevis, the femoral artery and the syrinx — that *Menura* and *Atrichornis* are closely related and, further, that they should be considered as Acromyodi Abnormales (= abnormal Oscines). It is not clear whether Garrod regarded his Menurinae (= *Menura* and *Atrichornis*, the Acromyodi Abnormales) as a separate suborder of the Passeres — most likely he did not. Contrary to Feduccia & Olson (1982:3), Garrod did not state that his Menurinae represented a distinct suborder, nor did he isolate them from the rest of Passeriformes. It is very clear that Garrod regarded the Menurinae as most closely allied to the normal Oscines. He placed both groups under the heading of Acromyodi (= Oscines), a group of equal rank with the Mesomyodi which contain all non-oscine passerines (Garrod, 1876:518). This arrangement differs from that proposed earlier by Garrod (1873:463) in which he included *Menura* in the Tracheophone Passeres on the basis of its carotid artery. Sibley (1974:66) was unclear in his reference to Garrod (1873 = 1873–4) in which he stated that Garrod united *Menura* and *Atrichornis* for the first time as the Acromyodi Abnormales. We find no mention of either genus in Garrod (1873–4) and suggest that Sibley confused reference to this paper either with Garrod (1873) or Garrod (1876). Sibley's discussion (1974:66) greatly confuses the whole issue, not only because it is unclear whether he referred to Garrod (1873) or Garrod (1876), but because Garrod's conclusions on the systematic position of the Menurae differ in these two papers, and because Newton (1875) could not have adopted Garrod's (1876) conclusion. To our knowledge, Garrod did not publish on the Menurae after 1876. Forbes (1881) summarized Garrod's contributions to the anatomy and systematics of birds.

Sclater (1880:345), in a vague, unsupported and undocumented statement, claimed that the Menurae are "the most anomalous forms of Passerine birds yet known" and placed them in the Pseudoscines as a separate group (= suborder) at the end of the passerine series. Sclater's conclusion is the basis for the separation of the Menurae as a suborder of the passerine birds, which was followed for the next century.

Forbes (1880:391) agreed with Garrod's system, and later (1881:26–27) disagreed strongly with Wallace's (1874) and Sclater's (1880) opinions that the Menurae should be separated from the Oscines and placed in their own suborder. It is not correct, as claimed by Sibley (1974:67), that Forbes (1881) did not argue for inclusion of *Menura* and *Atrichornis* in the Oscines. The group Acromyodi of Garrod and of Forbes are the Oscines (Garrod, 1876:518), and *Menura* and *Atrichornis* were regarded as abnormal Oscines by these two workers. In any review of the systematic history of birds, one must be most careful in noting the exact concept of taxonomic groups of earlier workers, especially when the same name is used for taxa of differing concepts. The Oscines of most modern authors are not the same as the Oscines of Garrod and Forbes. Subsequently, Forbes showed (1882a:544) that *Orthonyx* had a typical oscine syrinx (in his sense of the term) and, therefore, could not be closely allied to the Menurae. Forbes (1882b:571) reported on the syrinx of *Xenicus* and *Acanthisitta*, showing that they are Mesomyodian Passeres, and stated that, aside from the Pittidae, no additional member of the Mesomyodian Passeres is found in the Australasian region, thereby excluding the Menurae from this group. To our knowledge, this paper is the last published comment by Forbes on the affinities of these birds.

Until recently, the studies of Garrod and of Forbes have been the most important ones on the morphology and systematics of the Menurae. The subsequent history is complex and provides almost no new evidence supporting the different taxonomic conclusions until recent decades. Two major schools of opinion developed, one following the position of Garrod–Forbes and the other that of Wallace–Sclater. These differences appear to be rooted in a dispute between British morphologists (= prosectors of the Zoological Society of London) on the one side and systematists–biogeographers on the other.

The minority school of morphologists accepted the position of Garrod–Forbes. This included Beddard (1898:176–183), successor to Forbes as prosector of the Zoological Society of London, and Gadow in his volume on morphology and classification of birds (1893:270–282, see 277), but not in a shorter paper published the previous year (Gadow, 1892). Gadow (1893) quite clearly accepted the Garrod system, in which the Suboscines (= *Menura* and *Atrichornis*) are placed as a group under 'Passeres diacromyodals Oscines'. Gadow did not state why his arrangement of the Menurae differed in his paper of 1892 and in his volume of 1893. Nor is it clear which of these works represented his final ideas. An even greater problem exists for the classifications advocated by Sharpe who, in his major review of avian classifications (Sharpe, 1891a:84), placed the Menuridae in a monotypic order, the Menurae, and separated it from the Atrichiidae (= Atrichornithidae) which was placed in a distinct section

(= suborder ?) of the Passeriformes (Sharpe, 1891a:88). But in a catalogue of avian anatomical specimens, he (Sharpe, 1891b:xx) placed the Menuridae and the Atrichiidae in the Passeres Acromyodi or Oscines as a separate subdivision, the Passeres Abnormales, this being the Garrod–Forbes system. In 1901, Sharpe advocated yet another system in which he placed *Menura* in a separate order, the Menuriformes (Sharpe, 1901:3), and *Atrichornis* as the only family, the Atrichornithidae, in the Passeres Abnormales of the suborder Acromyodi, Passeriformes (p. 187). No comment is ever given by Sharpe for the changes in his placement of *Atrichornis* and *Menura*. The only possible summary of Sharpe's treatments of these genera is that he did not accept the Wallace–Sclater system. The major ornithologists of this century to accept the Garrod–Forbes arrangement are Evans (1900:491–493), Stresemann (1927–34:845) and Berlioz (1950:988–990). Evans and Stresemann placed the Suboscines (= Menurae) as a group, together with the Oscines in the division Diacromyodae which is of equal rank with the Mesomyodae. Thus, Stresemann accepted the arrangement of Gadow (1893), but it is a misrepresentation to state that he retained the 'isolated' position of the Menurae, as claimed by Sibley (1974:67). Berlioz placed the Menuridae and the Atrichornithidae in the suborder Oscines with the comment that these families are aberrant and constitute a connecting link between the Oscines (Acromyodae) and the Mesomyodae.

The majority school of thought started with Huxley (1867:472) who concluded that *Menura* stands apart from all other passerine birds. On the basis of skull morphology, he divided the Coracomorphae (= Passeriformes) into two groups, one containing *Menura* and the other the rest of the order. Parker (1875:306–309) agreed that *Menura* is primitive and isolated among the aegithognathous birds but was vague on the reasons supporting his conclusion. As mentioned earlier, Newton (1875:741) considered *Atrichornis* and *Menura* to be isolated within the passerine birds. Sclater (1880:345) concluded that these genera are the most anomalous passerines and placed them in a separate suborder, but with no support for his action. Newton (1885:41,47) did not accept the system of Garrod, contrary to Sibley (1974:66); instead, Newton adopted that of Sclater in which *Atrichornis* and *Menura* are placed in an isolated suborder. Stejneger (1885:459–461) agreed, claiming that the Menurae possess a number of characters of the Pici and arguing that they should be placed in a suborder separated from all other passerine birds. Fürbringer (1888:1538,1556) agreed with this position (see also the review by Gadow, 1888:181). As mentioned earlier, Gadow (1892:254) placed the Menurae in a separate order from the oscines and other non-oscines (except the Eurylaimidae which were placed in their own suborder). The only difference he cited between the Menurae and the oscines was the type of intestinal convolutions.

In his classic 'Dictionary of Birds', Newton (1896:524) supported his earlier position. Sharpe (1891a:84–88) took a somewhat unusual position by placing *Menura* in a separate order between the orders Eurylaimi and Passeriformes, which parallels the system of Gadow (1892), but he placed *Atrichornis* in a separate section (= suborder) at the end of the Passeriformes, separated from the Oscines by the Oligomyodae and the Tracheophonae.

As stressed by Sibley (1974:67–68), the influence of Newton, Sclater, Fürbringer and Stejneger was overwhelming, and most avian systematists thereafter followed the system in which *Menura* and *Atrichornis* are placed in a separate suborder of the Passeriformes. This is the arrangement advocated by Wetmore in the several editions of his influential classification (e.g., Wetmore, 1960; Wetmore followed Stejneger, 1885, closely in many details of his classification of birds which was originally developed and first published in 1929, following the earlier request of the Checklist Committee of the American Ornithologists' Union, see Wetmore & Miller, 1926), and by Mayr & Amadon (1951). It is also the system used in Peters's 'Check-list' (Traylor, 1979). Sibley (1974:67) erred, however, when he stated that no objection to the Newton–Sclater system has been raised since Forbes (1881). Sharpe (1891b), Gadow (1893), Evans (1900), Stresemann (1927–34:845), Berlioz (1950:988–990) and Bock (1972) accepted the Garrod–Forbes arrangement which constitutes a strong objection to the generally accepted Wallace–Sclater system.

No major advances were made until the 1970's when Ames (1971) published his major review of the syrinx and syringeal muscles in the Passeriformes. Ames gave less attention to the Menurae than to the other non-oscine groups, and said little about the taxonomic history of this suborder. On the basis of his morphological survey, Ames (1971:163–164) concluded that sufficient differences exist to maintain recognition of the suborder Menurae. He stated that the structure of the syringeal musculature and cartilages of the Menurae lies outside the range of variation shown by the Oscines. In his review of Ames, Bock (1972:902) concluded: "Instead of recognizing five suborders as does Ames (pp. 153–164), I would prefer to recognize only three — the Furnarii, the Tyranni and the Oscines (his Passeres and Menurae). I cannot find any strong reason to maintain the Menurae as a distinct suborder, as its syringeal morphology is basically that of the Oscines." Bock pointed out (p. 901) that Ames never discussed the syringeal aponeurosis which is present only in his Menurae and his Passeres (= the Oscines) and may be responsible for both the basic similarities of the syringes of these groups and their differences from the syringes of other passeriform groups.

Sibley (1974) provided the first new evidence in almost a century to support the oscine relationships of *Menura*; his work was based on isoelectric focusing of egg-white proteins. Sibley's paper is significant in that it focused attention on the Menurae, and argued for oscine relationships of these birds. He concluded that

Menura is probably most closely related to the Ptilonorhynchidae-Paradisaeidae complex. These conclusions were reinforced by Sibley (1976). Subsequently, using DNA–DNA hybridization, Sibley & Ahlquist (1985, in press) were able to compare *Menura* and *Atrichornis* with other passerine birds. They concluded that these two genera are closely allied, and that the Ptilonorhynchidae, but not the Paradisaeidae, are the closest relatives of the Menuridae-Atrichornithidae complex. They do not discuss the reasons for the differences between their conclusions and the earlier ones of Sibley (1974, 1976).

In a complex series of papers, Feduccia (1975a, 1975b, 1976, 1977, 1979) described the morphology of the bony stapes in passerine and other birds, and discussed its value for classifying birds. The results of these studies are difficult to assess because of major modifications of his conclusions without new factual information. More recently, Feduccia & Olson (1982) compared the Menurae to the Rhinocryptidae of the Neotropics. In this paper, they were most concerned with the question of whether the Menurae are related to the Ptilonorhynchidae, and they showed that these groups are not especially similar osteologically. Their paper is interesting because it puts forth, once again, a strong suggestion for relationships between the Menurae and the Rhinocryptidae, an idea that had become dormant about 100 years ago.

Taxonomic Analysis

Because *Atrichornis* (Atrichornithidae) and *Menura* (Menuridae) are currently placed in Peters's 'Check-list' in a separate suborder, Menurae, listed just before the Oscines (Mayr, 1979), we will use this arrangement as the basis of our taxonomic analysis.

Group hypotheses. Based on earlier ideas on the relationships of *Atrichornis* and *Menura*, a series of group hypotheses (Bock, 1981) about these birds can be offered. We accept the conclusion that these birds are members of the Passeriformes, although several workers at the end of the last century placed one or both genera in a separate order. The group hypotheses are:

(1) *Atrichornis* and *Menura* are each other's closest relatives (sibling groups) and hence constitute a monophyletic group.

(2) *Atrichornis* and *Menura* are members of the suborder Oscines (Acromyodi), as recognized in Peters's 'Check-list'.

(3) *Atrichornis* and *Menura* are members of the suborder Tyranni (Mesomyodi), as recognized in Peters's 'Check-list'. (We are not here concerned with the question of whether this suborder actually consists of two distinct groups, the Furnarii and the Tyranni, as recognized by Ames, 1971. If one regards both of these groups as suborders, then the hypothesis can be rephrased to ask whether the Menurae are members of the Furnarii.)

(4) *Atrichornis*, *Menura* and the Ptilonorhynchidae form a monophyletic group within the Oscines.

(5) *Atrichornis*, *Menura* and the Rhinocryptidae form a monophyletic group within the Tyranni.

(6) *Atrichornis* and *Menura* constitute a monophyletic group of unknown affinities within the Oscines.

(7) *Atrichornis* and *Menura* are sufficiently distinct to be placed in monotypic families, the Atrichornithidae and the Menuridae.

(8) *Atrichornis* and *Menura* are primitive within the Oscines.

(9) *Atrichornis*, *Menura* and the Rhinocryptidae are all primitive groups within the Passeriformes and are closely related phylogenetically, *Atrichornis* and *Menura* being the most primitive members of the Oscines and the Rhinocryptidae being the most primitive members of the Tyranni.

The first seven are classificatory hypotheses about groups, and the last two are phylogenetic hypotheses about groups and must be tested somewhat differently (Bock, 1981).

Character analyses. The evidence presented by the several authors in this monograph and by other workers (Ames; Sibley; Feduccia & Olson) will be summarized.

THE SYRINX. As soon as the syringes of *Atrichornis* and *Menura* were described by Garrod (1876), it was clear that these birds agreed most closely with the Oscines in syringeal morphology. This conclusion was further strengthened by the monograph of Ames (1971) on the passerine syrinx. *Atrichornis* has a weakly fused syringeal drum but *Menura* has unfused syringeal cartilages. Both *Atrichornis* and *Menura* possess a syringeal aponeurosis which appears to be homologous with that of the Oscines. This aponeurosis is lacking in all other passerine groups. Although the syringeal aponeurosis appears to be fundamental to the morphological organization and to the function of the syrinx, Ames scarcely mentioned it. The syringeal muscles present in *Atrichornis* and *Menura* appear to be homologous to those present in the Oscines. We agree with Sibley (1974:72) that the medial fibres of the M. bronchotrachealis anticus in *Atrichornis* are homologous with the M. bronchialis anticus, pars medialis of the Oscines. Basically, we agree with the analysis of syringeal morphology and evolution presented by Sibley (1974:69–73); this is not special pleading, as characterized by Feduccia & Olson (1982:4). Little is known about how sound is produced by the avian syrinx, and nothing is known about the correlation between variation in syringeal structure as seen in passerine birds and the sounds produced by these birds (Gaunt & Gaunt, 1985). Therefore, we do not believe that it is possible to determine, at this time, whether the menurine syrinx is primitive or advanced, compared with the typical oscine syrinx. We find no structural features or arguments precluding the conclusion that the menurine syrinx is advanced, having reduced the musculature slightly and decreased considerably the degree of fusion of the tracheal rings comprising the oscine drum. As Ames stated (in Sibley 1974:73–74): "no syringeal data that says that they [*Menura* and

Atrichornis] can't [be derived from the Oscines]", and "Virtually any oscine syrinx can be derived from almost any other, and without too much change in muscles."

Sibley (1974:72–73) made a most important point when he stressed that the amount of observed variation in syringeal musculature in passerine birds depends very largely on the detail in description. As description becomes less detailed, the amount of variation in a feature within a taxonomic group decreases. For example, variation in syringeal muscles in the Passeriformes would disappear completely if the level of description were limited to statements of the presence or absence of syringeal muscles. A major difficulty in assessing the significance of differences in syringeal morphology between the Menurae and the Oscines is that we still lack a detailed survey of syringeal morphology in the Oscines, a point stressed by Sibley.

BONY STAPES. In a series of papers, Feduccia described the bony stapes of a number of avian groups and argued that this feature is a useful taxonomic character. Among passerine birds, the stapes has two basic morphologies. One is a flat footplate with a straight, central bony shaft, and the other is an expanded bulbous footplate extending well along the shaft with one or more large fenestrae and an offset bony shaft. The first morphology is found in many avian groups and in reptiles; it is presumed to be primitive. The second morphology is one of the few advanced avian conditions. Nothing is known about the functional properties and possible adaptive significances of the major stapedial morphologies in birds.

Feduccia (1975a), agreeing with Sibley (1974), concluded that the lyrebirds are oscine and are likely to be close to the bowerbird/bird-of-paradise group. He also concluded that the Acanthisittidae are probably members of the Oscines.

In his major review, Feduccia (1975b) repeated these conclusions in a somewhat different form. He argued that the stapes found in the Tyranni plus Eurylaimidae and that found in the Alcediniformes (Meropidae, Alcedinidae, Todidae, Momotidae and Trogonidae) are homologous as a bulbous stapes with a marginal membrane. The alcediniform stapes differs from the tyranniform stapes in the shape of the base and position of the shaft (Feduccia, 1975b:26). Feduccia concluded that the Passeriformes (as usually recognized) are polyphyletic, with the suboscines (Tyranniformes = Tyranni plus Eurylaimi) related to the Alcediniformes and not to the Passeriformes. Further, he concluded (Feduccia, 1975b:33) that it was improbable that *Menura* and *Acanthisitta* are suboscines, backing off somewhat from his earlier conclusion. Subsequently, Feduccia (1977:19) reaffirmed that the Menurae and the Acanthisittidae are Oscines (= his Passeriformes) but this conclusion was not based on stapedial morphology. He stated only that possession of the primitive stapes in these groups shows that they are not suboscines (= his Tyranniformes).

In a later paper, Feduccia (1979:691) reversed his opinion on the homology of the suboscine and the alcediniform stapes as one with a rounded, bulbous, fenestrated footplate. He now concluded that these are two distinct types of stapes which are not homologous, but are similar only through convergence. The minor difference in the shape of the footplate and position of the shaft mentioned in his earlier paper (Feduccia, 1975b:26) was now considered to be a major difference, showing that these stapes cannot be homologous. This conclusion appears to be based on the finding that sperm of the oscines and that of the suboscines are morphologically similar enough to be homologous as bundled sperm with a tripartite structure of its undulating membrane (Henley, Feduccia & Costello, 1978; see also McFarlane, 1963).

Feduccia & Olson (1982) showed that the Menurae and the Acanthisittidae both possess the typical primitive avian stapedial morphology. Yet they assume *Acanthisitta* and *Xenicus* to be oscines, but that *Atrichornis* and *Menura* are either not allied to other suboscines or that these genera evolved before the advent of the derived suboscine type of stapes. No additional evidence is presented to support either interpretation of the homology of the stapes of the Acanthisittidae and the stapes of the Menurae with that of the Oscines. It appears that the conclusion of Feduccia & Olson (1982) on the homology of the stapes of the Menurae and of the Oscines, which is directly opposite to the conclusion reached by Feduccia (1975a), is based strictly on their argument that the Menurae are not related to the Ptilonorhynchidae, but may be related to the Rhinocryptidae. We hold their conclusions on the homology of the stapes to be based on special pleading.

It is difficult to reach conclusions on the homologies of the various morphologies of the stapes and their taxonomic value. Clearly, the stapedial condition with a flat footplate and straight, thin stem has little taxonomic value because it is found without significant variation in many groups of birds and in reptiles. We would agree with Feduccia that this shape appears to be primitive.The stapedial morphology with a bulbous, fenestrated footplate appears to be advanced. But we do not believe that a strong argument has been presented showing a lack of homology between the stapes with a bulbous, fenestrated footplate in the suboscines (Tyranniformes) and that in the Alcediniformes. Whether these groups have evolved the rather similar bulbous condition of the stapes independently must remain an open question at this time.

PTERYLOSIS. Details of the body pterylosis are reported by Clench (1985), and of the wing and tail pterylosis by Morlion (1985). Although it is possible to determine homologies of many of the attributes of the pterylosis between the Menurae and other passerine birds, it is not easy to establish ancestral-descendant sequences. No basis exists on which to conclude that the large number of remiges and rectrices in *Menura* is primitive. And it is difficult to evaluate the pecularities seen in the wing and tail pterylosis of *Atrichornis* and *Menura* because of the absence of sufficient comparative studies.

OSTEOLOGY. Comparisons of the skeleton have been used traditionally in avian systematics because many characteristics can be examined readily and because the skeletons of many avian groups have been examined, thereby providing a broad comparative foundation. The major problem is that homologies between attributes of the skeleton are far more difficult to establish that usually believed, and primitive or advanced conditions are usually impossible to ascertain. This is especially true for the skeleton of passerine birds, in which parallel evolution and reversal of evolutionary changes run rampant.

Sibley (1974:68) claimed that skeletons of *Menura novaehollandiae* and of *Chlamydera lauterbachi* "are virtually identical except for the shape of the posterior margin of the sternum, the absence of an ossified hypocleideum in *Menura* and the difference in size of all elements." Bock (1985) stated that, aside from the similarity of the free lacrymal bone of the Menurae and of the Ptilonorhynchidae, the cranial osteology of these groups differs markedly within the range of variation seen in passerine birds. Feduccia & Olson (1982:16) concluded that the "osteology of these two birds [= *Menura* and *Chlamydera*] is actually extraordinarily divergent, especially in light of the relative osteological homogeneity of the vast majority of Passeriformes."

Further, Feduccia & Olson (1982:16) stated that, in many features of the skeleton, "the Menurae are much more similar to the Rhinocryptidae than to any other passerine group. Most of the characters shared by these two groups are not found elsewhere in the Passeriformes." Many of the similarities cited are in the structure of the wing and the leg. Feduccia & Olson did not discuss the possibility that these similarities may be parallelisms related to reduction of flight and increased terrestriality of both groups. Rich, McEvey & Baird (1985) discussed this possibility in detail and concluded that the observed skeletal similarities in the Menurae and the Rhinocryptidae may be convergent adaptations to a terrestrial way of life. We would agree. Even the keel on the dorsal edge of the upper jaw of *Atrichornis* and of some rhinocryptids may be convergent to terrestrial feeding. Smith (1976:130) reported that *Atrichornis* scratches for food by flicking the ground litter aside, using its bill. The dorsal ridge on the upper jaw could be an adaptation for this feeding behaviour.

CRANIAL MYOLOGY. The tongue muscles provide some interesting clues to the phylogenetic position of *Atrichornis* (Bock, 1985). Five aspects of the tongue musculature and one of the hyoid skeleton appear to be advanced, compared with those seen in other passerine birds. None of these are unique. One feature of the tongue musculature is still somewhat primitive. Although little is known about the food and feeding behaviour of *Atrichornis* (Smith, 1976), the scrub-bird presumably feeds on insects and other small invertebrates living in the forest floor litter (Smith & Calver, 1984). Most of the advanced attributes of the tongue musculature are not obviously correlated with feeding on invertebrates in the forest floor litter.

APPENDICULAR MYOLOGY. The musculature of the wings and legs of the Menurae possess a number of features not found in other passerine groups (Raikow, 1985). The structure of the M. flexor perforatus digiti IV is homologous with that of the oscines and not with that of the suboscines. The appendicular myology of the Menurae does not show any particular homologies with that of the Ptilonorhynchidae, nor to any other oscine group.

The reduction in flying ability is correlated with a number of features in the pectoral morphology, such as decrease in the size of the flight muscles, reduction of the clavicles, and shortened wing length. Specializations are found in the pelvic myology associated with increased terrestrial habits. These pelvic changes are especially developed in *Menura*. Although a thorough functional-adaptive analysis is not available for the changes in the skeletomuscular systems of the forelimb and the hindlimb, the most reasonable conclusion is that these features are advanced in the Menurae compared to other passerine birds. No one would doubt that primitive passerine birds flew and that development toward flightlessness is derived. Feduccia & Olson (1982:18), however, argued for "the interesting possibility that the original passerine adaptations were for life on the ground and that this order as a whole, the epitome of 'perching' birds, is only secondarily adapted for an arboreal existence." Rich, McEvey & Baird (1985) provided a strong counterargument. We find this latter discussion far more convincing, especially in view of the evolution of many diverse terrestrial groups among the passerine birds.

BIOCHEMICAL CHARACTERS. Sibley (1974) provided the first new evidence in recent years indicating a relationship between *Menura* and the Oscines. Using isoelectric focusing of egg-white proteins, he concluded that these proteins in *Menura* agreed closely with those in the Paradisaeidae and the Ptilonorhynchidae. In later works, Sibley & Ahlquist (1985, in press), using the technique of DNA–DNA hybridization, stated that the Menurae were closely related to the Ptilonorhynchidae, but not to the Paradisaeidae. Unfortunately, they did not discuss why the earlier studies using egg-white proteins indicated a close relationship between the Paradisaeidae and the Ptilonorhynchidae and, hence, between both of these groups and the Menurae.

LIFE HISTORY. Aspects of the life history of *Atrichornis* and *Menura* have been reviewed by Smith (1976). Information on the diet of *Atrichornis clamosus* is provided by Smith & Calver (1984). *Menura novaehollandiae* is reasonably well known, and most of our knowledge about the life history of *Atrichornis* comes from recent studies on the Two Peoples Bay population of *A. clamosus*. These genera agree in many aspects of breeding, courtship displays, song and terrestrial way of life. Some of the similarities are striking in view of the great difference in body size of the two genera, and considering the courtship

specializations of *Menura*.

Conclusions. Using the information available in the several studies of this monograph and the above summary, we would like to examine the nine group hypotheses presented earlier.

(1) We accept the hypothesis that *Atrichornis* and *Menura* are each other's closest relatives and constitute a monophyletic taxon. All of the evidence in this monograph supports this hypothesis, as do Sibley & Ahlquist (1985, in press) and Feduccia & Olson (1982). Most earlier workers, following Garrod (1876), accepted this conclusion although Sharpe (1891a; 1901) placed *Menura* in a different order from the Passeriformes.

(2) We accept the hypothesis that *Atrichornis* and *Menura* are members of the suborder Oscines as recognized in Peters's 'Check-list'. This is supported by the structure of the syrinx, as first pointed out by Garrod (1876) and commented on by Bock (1972). We believe that the detailed homologies of the syringeal musculature, as well as that of the syringeal aponeurosis of the former Menurae and of the normal Oscines, provide strong support for this hypothesis. Raikow (1985) showed that the structure of the M. flexor perforatus digiti IV is homologous in the former Menurae and the normal Oscines (see also Raikow, 1982, when he discussed the monophyly of the Passeriformes). Sibley (1974, 1976) and Sibley & Ahlquist (1985, in press) demonstrated close similarity among the egg-white proteins and DNA–DNA hybridization of the former Menurae and the normal Oscines. Most of the earlier conclusions for a very isolated taxonomic position of the Menurae in the Passeriformes, or even their placement in a separate order, were based on peculiar features of *Menura* which reflect its large size, terrestrial habits and courtship displays.

(3) We reject the hypothesis that *Atrichornis* and *Menura* are members of the suborder Tyranni (= suboscines of Feduccia & Olson, 1982), as recognized in Peters's 'Check-list'. Such a relationship was advocated by Feduccia & Olson (1982), following up on the old suggestion by Sclater (1874) and Wallace (1874) that *Atrichornis* and *Menura* may be members of the Rhinocryptidae. We believe that the similarities between the Menurae and the Rhinocryptidae cited by Feduccia & Olson (1982) are most likely the results of convergence (see Rich, McEvey & Baird, 1985). No convincing set of homologous features supports this hypothesis, and many oppose it strongly, e.g., those homologues supporting the hypothesis that the Menurae are members of the suborder Oscines.

(4) We cannot accept the hypothesis that *Atrichornis*, *Menura* and the Ptilonorhynchidae form a monophyletic taxon within the Oscines. The only evidence that seems to support this hypothesis comes from the biochemical studies by Sibley (1974, 1976) and by Sibley & Ahlquist (1985, in press). The bulk of the evidence from the pterylosis, osteology and myology of these birds presented in this monograph and by Feduccia & Olson (1982) does not support this hypothesis or, at best, is only suggestive. However, none of the morphological evidence serves to falsify this hypothesis at this time, so that it cannot be rejected.

(5) We reject the hypothesis that *Atrichornis*, *Menura* and the Rhinocryptidae form a monophyletic group within the Tyranni for the same reasons given above in rejecting hypothesis 3.

(6) We accept the hypothesis that *Atrichornis* and *Menura* form a monophyletic group of unknown affinities within the Oscines. These two genera possess a number of unique features that separate them from other Oscines. Moreover, they do not possess any features that indicate strongly a relationship with any other oscine group, except, of course, the biochemical evidence suggesting an affinity with the Ptilonorhynchidae (see hypothesis 4). This lack of evidence may simply be the result of insufficient comparative studies and it may change in the future. It is not clear whether the suite of features unique to *Atrichornis* and *Menura* are largely the result of terrestrial habits and decreased flight abilities or are also strongly indicative of a close relationship. And it is not known whether a number of these features will be found in other specialized terrestrial passerine birds.

(7) We accept the hypothesis that *Atrichornis* and *Menura* are sufficiently distinct to be placed in monotypic families, the Atrichornithidae and the Menuridae. The differences in size, feeding habits, courtship displays and numerous morphological features support this hypothesis strongly. These differences are compatible with differences among many other families of passerine birds. It should be noted that Sibley & Ahlquist (1985, in press) place *Atrichornis* and *Menura* in the same family, the Menuridae, based strictly on the size of the delta $T_{50}H$ value for the DNA–DNA hybridization between the two genera.

(8) We do not accept the hypothesis that *Atrichornis* and *Menura* are primitive within the Oscines. These two genera possess a number of derived specializations such as decreased flying ability, terrestrial habits, morphological features of the tongue musculature, etc. At this time, it is not possible to establish the particular syringeal features of these genera as primitive or advanced. Analysis of the evolutionary history of the Oscines, and determination of presumed primitive groups, cannot be accomplished with certainty at the present state of our knowledge.

(9) We reject the hypothesis that *Atrichornis*, *Menura* and the Rhinocryptidae are all primitive groups within the Passeriformes and are closely related phylogenetically. We cannot speak about the phylogenetic position of the Rhinocryptidae within the suboscines, but not accepting hypothesis 8 determines our decision on the current hypothesis. We would add that we would reject the hypothesis suggested by Feduccia & Olson (1982:17–18) that the original passerine adaptations were for life on the ground.

In conclusion, we would place the Atrichornithidae

and the Menuridae in a superfamily, the Menuroidea, of unknown affinities within the suborder Oscines. The Menuroidea, as we delimit them, differ from the concept of the Menuroidea advocated by Sibley & Ahlquist (1985), which includes the Climacteridae and the Ptilonorhynchidae, as well as the lyrebirds and the scrub-birds. The Menuroidea, as we delimit them, appear to be specialized for a semivolant, terrestrial mode of life. It seems reasonable to suggest that the Atrichornithidae and the Menuridae are relict members of an earlier, more diverse radiation of Australasian oscine birds. The Ptilonorhynchidae and others may also be part of this early radiation, but we do not feel that the available evidence is sufficient to resolve the detailed relationships within the major early radiations of Australasian oscine birds. This idea of an early radiation is not new, but has been postulated by a number of other workers. We believe that the contributions to this monograph have provided considerable evidence supporting this conclusion. We consider, however, that it is premature to speculate on possible causes for the reduction of the presumed earlier radiation of menurine birds.

Conservation Efforts

The species of *Menura*, and especially of *Atrichornis*, are endangered or threatened throughout much of their range. *Atrichornis clamosus*, believed for many decades to be extinct, survives in only one small locality at Two Peoples Bay, east of Albany, Western Australia. Scrub-birds and lyrebirds are very secretive birds, specialized for ground dwelling in thick growth. They are easy to hear because of the loud songs of the males but difficult to see because of their shy habits and the dense habitat in which they live. These habits are not unique for Australian birds; they are also found in the chowchillas (*Orthonyx*), whipbirds (*Psophodes*), fairy wrens (*Malurus*), grass wrens (*Amytornis*), bristlebirds (*Dasyornis*) and the pilotbird (*Pycnoptilus floccosus*). The menurines are not necessarily driven out by human contact, as demonstrated by the long-studied Superb Lyrebirds of Sherbrooke Forest east of Melbourne (Pratt, 1974; Smith, 1951). The slow reproductive rate (one or two eggs per year) and long incubation and fledgling periods of chicks of *Atrichornis* and *Menura* may be important factors contributing to their decline. These extreme terrestrial habits may also make these birds easy prey for feral cats and introduced foxes.

It is quite possible that the scrub-birds and lyrebirds are evolutionary relicts and, as remnants of an earlier larger radiation, are facing extinction because of competition from other avian species and/or because of modified environmental conditions. These possibilities would make conservation efforts far more difficult. Special efforts would be required to preserve large tracts of habitat suitable for these species. More studies should be undertaken without delay to learn the ecological requirements of each species because this information is essential for further conservation actions. The undertakings at Two Peoples Bay for the population of *Atrichornis clamosus* appear to be an excellent model for similar efforts with the other three species of the Menuroidea.

Scientific Cooperation

When the *Atrichornis* project was in its initial planning stages, the problem to be addressed was having an anatomical specimen of an endangered species, *Atrichornis clamosus*, for which very little was known about its morphology and systematic position. The question was, how should studies be arranged so that maximum information could be obtained from a single specimen. Clearly, the answer was to seek out the needed expertise and to arrange the sequence of study in a suitable way. It was necessary to obtain cooperation among enforcement officers and scientific researchers in Australia and abroad, mainly in the United States. After individual workers agreed to take part in the study, they had to stop other work and turn to the *Atrichornis* specimen when it arrived. Dr Morlion travelled to the United States to do her investigations because of the dangers and difficulties in shipping the specimen to Europe and back again to North America.

The resulting monograph is proof of the success of this cooperative effort. The results will benefit Australians interested in the evolutionary biology and preservation of their avifauna. These results are also of importance to international ornithologists interested in avian morphology and systematics. This study served to bring together a number of ornithologists from Australia, Belgium and the United States who may have never met or only rarely see each other at International Ornithological Congresses. We hope that the *Atrichornis* study will serve as a role model for future cooperative investigations on the morphology and systematics of little-known species of birds.

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Form and Decoration of Arrows from the Highlands of Papua New Guinea

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ABSTRACT. This study concerns the form and decoration of arrows from the highlands of Papua New Guinea. The morphology of a sample of 834 arrows is described. The decorative carvings on fore-shafts and heads are analysed in terms of 13 elements and variants of these. The combinations of elements into design patterns is described and their geographic distribution analysed. Variations in both morphology and design are found to correlate with language family boundaries for the most part, but the most clearly marked boundary lies between Central and West Central language family areas.

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KEYWORDS: arrows, form, decoration, Papua New Guinea, language boundaries, physiographic boundaries.

The use of bows and arrows for fighting, hunting and display is almost universal in Pacific islands' cultures, and is certainly so throughout the highlands of Papua New Guinea. Being among the most common artefacts and being, to many European eyes unusual and decorative, arrows have been frequently collected. Museums in many parts of the world hold large collections of arrows, which have, however, rarely been the subject of detailed study. This work is a contribution both to the systematic description of these artefacts and to an understanding of the relationship between the distribution of arrow forms and designs, and geographic and linguistic entities.

This study was begun originally as an M.A. thesis (Bush, 1976). The present publication has been extensively amended and re-written, especially in the light of new interpretations of the linguistic data. There has, however, been little modification of the analyses of arrows.

STUDY AREA

Geography. The highlands of Papua New Guinea cover an extensive area of the cordillera that stretches for 960 km and forms the 'backbone' of Papua New Guinea and extends into Irian Jaya. It is a complex system of broken ranges, forming mountain barriers which frequently separate broad upland valleys, and is the watershed for many river systems flowing north, south and east. The ranges that form the cordillera rise to great heights — the highest, Mt Wilhelm at 4,438 m, being part of the Bismarch Range, an arm of which forms the Sepik-Wahgi Divide. Mt Kubor, 4,290 m, is the highest mountain on the southern side of the cordillera that partly encloses the Wahgi and Chimbu River systems.

The eastern boundary of the highlands is relatively well defined by the steep scarp known as the Ramu-Markham Fall. In strict geographic terms the western end lies in Irian Jaya at about 135°E. This study is, however, concerned with that part of the cordillera which lies east of the Papua New Guinea – Irian Jaya border, and particularly with that lying east of the Strickland Gorge.

Within these geographic limits is an important physiographic division, the Chimbu–Asaro Divide. This mountain chain runs roughly north-south, separating the Asaro River valley to the east, from the Chimbu River system to the west. This divide is considered a significant boundary in cultural terms.

Linguistics. Between the Asaro and Chimbu valleys there is a "linguistic break' (Read, 1954:7). This break

between East Central and Central language families closely follows, in part, the Chimbu–Asaro Divide (McKaughan, 1972; Würm, 1975: 563, Fig. 1). The Chimbu languages on the western side of the Divide are different in phonetics and vocabulary to those on the eastern side, and indicate a relationship to languages of the Hagen area and westwards. These western languages (i.e. the Hagen–Wahgi–Jimi–Chimbu group) are cognate but not mutually intelligible.

Settlement pattern. Both Read (1954:12) and Brookfield & Hart (1971:222–4) record that settlement patterns differ on each side of the Chimbu–Asaro Divide. To the east are found nucleated villages, whilst in the Chimbu area and further west, residence is in the form of dispersed settlements.

Stone-axe quarries and axe blades. Eleven stone-axe quarries investigated by Chappell (1966:97, 111–2) and two by M. Strathern 1966:118) constitute the main quarries in the central highlands. Chappell (1966:97) places twelve of these on the western side of the Chimbu–Asaro Divide, with the remaining one at Kafetu on the Divide. There are no quarries east of Kafetu, and stone axes are not made from quarried material east of the Divide.

According to Strathern (ibid.) the types of axe-blades produced are also different. Polished axe-blades, planilateral in section, come from the twelve quarries west of the Chimbu–Asaro Divide, whilst the quarry at Kafetu 'seems only to have produced blades of a lenticular section.' Planilateral axes are not manufactured in the east.

Archaeology. Among 6 archaeological sites (R. S.Bulmer, 1964, 1966,1976; White, 1965, 1967a, 1972), Yuku, Kiowa, and Nombe (Niobe) to the west of the Divide contained flaked waisted blades, whilst Kafiavana, Aibura and Batari to the east did not. The meaning of this dichotomy is at present unknown. There are also minor differences in the flaked stone artefacts.

Languages. According to Würm (1975), highland's languages are all non-Austronesian (Papuan), and are members of two stocks:

1. East New Highlands stock comprising Eastern, East Central, Central, West Central and Kalam families, and Wiru and Kenati family-level isolates;

2. Central and South New Guinea stock, which includes Duna and Ok families.

The distribution of these languages is given in Figure 1. The Central and South New Guinea stock is found in the western part of my study area (Duna family) but extends further west into Irian Jaya, and south into the Fly River Lowlands.

Lexicostatistically, Duna is considered a link between the two stocks with heavy borrowing from Huli of West Central family, yet structurally shows similarities to three families of Central and South New Guinea stock (Würm, 1975: 395).

The relationship of Oksapmin family to other families is unclear; Würm regards it as a sub-phyulum level isolate. Healey (pers. comm.) feels that almost all of the similarities with Ok are due to borrowings in both directions between Oksapmin and Bimin, a family of the Mountain Ok sub-family.

Recent theories on language movements in Papua New Guinea (Würm, 1975) indicate an early movement, through much of mainland New Guinea from west to east, of daughter languages of the trans New Guinea phylum proto-language. Then, during the last 5,000 years, movements from east to west seem to have been responsible for similarities in many highlands languages. These include a migration from the Finisterre area (Huon family) to Telefomin area (Ok family); the relationship is based mainly on typological similarities (e.g. in verb structure and usage). Healey suggests this relationship is probably genetic, though remote.

In this study I have made use of material from all the above-mentioned families and isolates (except the Kalam family and the Kenati family-level isolate). I have also used material from the area of the Daribi language family (Karimui), because arrows and ethnographic data were available from this family which is distantly related to east New Guinea highlands stock. I also used, as a comparison, arrows of the Aiome people (Aian language family) who live on the middle Ramu River. Details of arrows within each family area are given in my thesis (Bush, 1976: 171–216).

Geography and Language

The relationship between physiographic and language boundaries in the highlands makes an interesting study, but only the main boundaries that occur within the study area are summarized here. Physiographic and language boundaries that show close correspondence are:

1. Chimbu–Asaro Divide and boundary between East Central and Central language families.

2. Yuat–Mt Hagen–Kaugel River and boundary between Central and West Central language families.

3. Ramu–Markham Fall and the eastern boundary for families of East New Guinea Highlands stock.

The Strickland Gorge appears to be simply a major physiographic boundary within the highlands proper. It shows no correspondence with boundaries of language families that make up the northern group of Central and South New Guinea stock, although it forms part of the boundary of the Oksapmin sub-phylum level isolate.

To summarize the language situation in the highlands as it appears at present, there seem to be two roughly north-south physiographic boundaries, the Chimbu–Asaro Divide and the Yuat–Mt Hagen–Kaugel River complex, which divide highlands languages into Eastern, Central and West Central groups. A further group extending westwards from West Central family boundary includes Duna and Ok families of Central and South New Guinea stock.

Role of Arrows in Highlands Cultures

Arrows (and bows) are carried by a highlands man almost as part of himself, wherever he moves outside

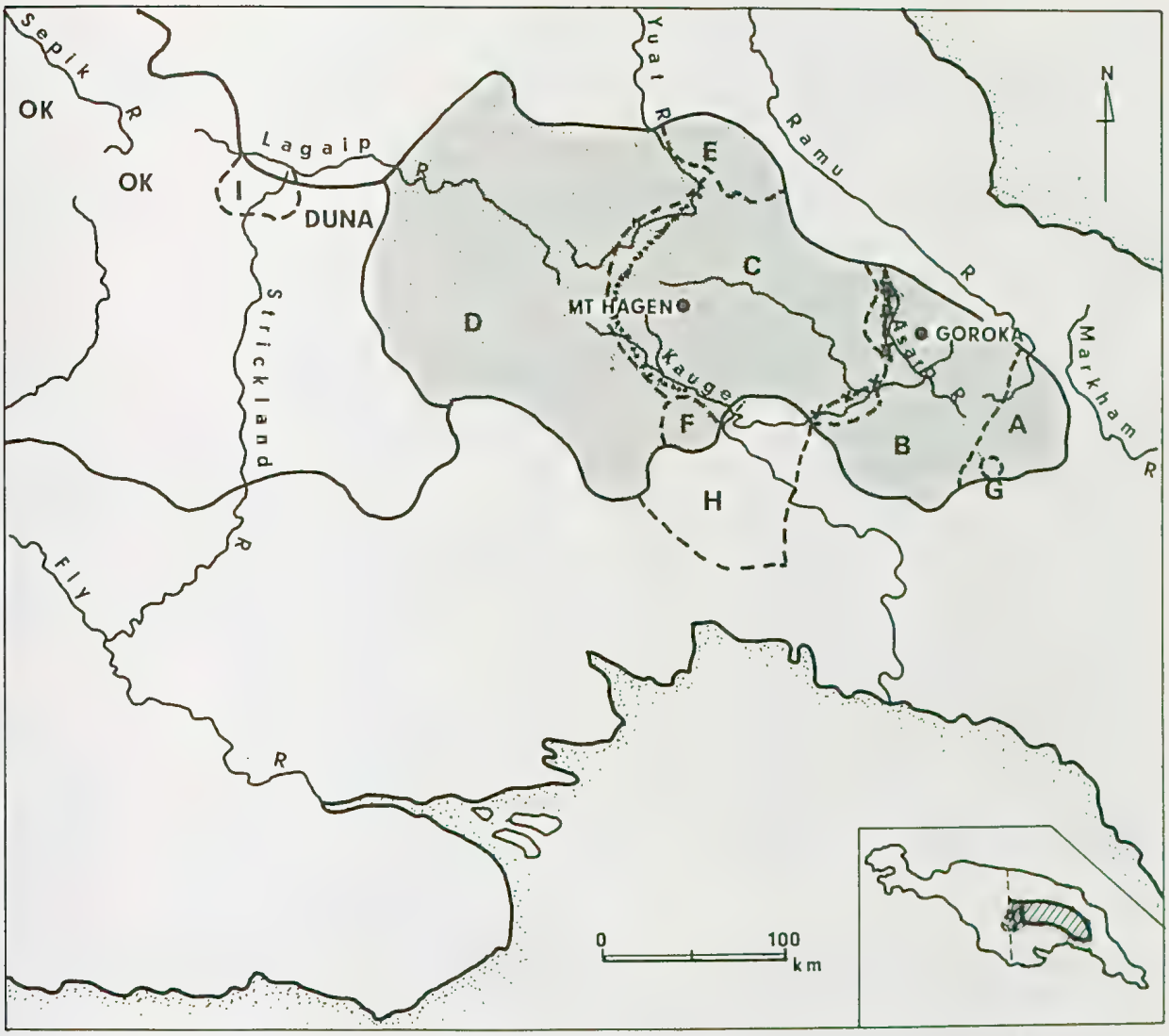


Fig. 1. New Guinea highlands language groups. **Inset:** study area, including East New Guinea Highlands stock and Central and South New Guinea stock areas. **A**: Eastern; **B**: East Central; **C**: Central; **D**: West Central; **E**: Kalam; **F**: Wiru family-level isolate; **G**: Kenati family-level isolate; **H**: Teberan-Daribi (Karimui); **I**: Oksapmin sub-phylum-level isolate;

———	Stock boundary	-x-x-x-x-x-	Chimbu-Asaro Divide
Shaded area	East New Guinea highlands stock	.....	Suggested major boundary between Central and West Central arrow designs

his village. It would seem this behavioural norm gives him a sense of security, and indicates to others his manhood status, while the arrow types he carries could point to the purpose of his sojourn away from his village — hunting, fighting or to attend ceremonies elsewhere. At ceremonies such as marriage or pig feasts, men usually carry their most ornate arrows to display at the gathering and gain prestige. At such ceremonies, the relationship between clans is enhanced by presentations and gifts of elaborately carved arrows.

From personal observation at Isale village, Ialibu, and Yagusa village, Henganofi, the manufacture of an arrow by a specialist arrow-maker becomes a male social gathering where clan gossip is exchanged, with the arrow-maker joining in as he continues working. It should, however, be noted that all highlanders know how to manufacture arrows, and traditionally most did so.

In 1974 I visited several highlands villages and, where possible, met specialist arrow-makers, all of whom were older men. From an interpreter to whom I posed questions about these men, I learned that an arrow-maker's position within the village community was no different from any other member of his clan. However, his superior ability and technical skill in carving designs on arrows is recognized, and gains him prestige. He is an expert whose work is identifiable from that of other arrow-carvers, even though others may copy the designs he uses. He is the person to whom other clansmen come when they require an arrow for a special purpose — a marriage ceremony, *Moka*, pig feast or, in the not-so-distant-past, to kill a specific person.

Arrows emphasise the difference between the roles of male and female within the clan. The making and use of arrows is the exclusive right of males, but in some highlands areas the treatment of raw material to make colour pigments used in arrow designs is done by clan females expert in this work.

Arrows play an important part in social organisation. Special arrows are manufactured by the kin of a murdered person, to use against the person who committed the crime and his kin in 'pay-back' killings. These arrows are made whilst sitting in groups, and 'magic talk' is intoned over each arrow when completed. It is then sheathed and put aside for its later use (Bush, 1976). This 'special purpose' arrow manufacture emphasises clan solidarity.

In pre-contact times, arrows were sometimes used as items of exchange, within and outside clan boundaries. I was told by specialist arrow-maker, Manda Pumuye of Isale village, that in the pre-contact era he traded his arrows to the Mendi people for salt and Kina shell.

In hostilities, arrows are the main weapons used by highlanders to defend their territorial rights, in 'pay-back' killings, in fights resulting from the stealing of pigs and women, failure to pay compensation, or any other infringement of clan rights. As yet, no European-introduced implement has been adopted into highlander's material culture to such a degree as to 'oust' the arrow from its traditional usage as a hunting — fighting weapon. Even in the present (1985), in spite of government bans, tribal fights still occur in the highlands, with arrows the main weapon used.

ARROWS

Sources of data. For the purpose of this study I have examined, measured component parts, tabulated data and made accurate drawings of designs on 834 arrows from as many different physiographic and linguistic areas of the New Guinea highlands as was possible. The populations of arrows studied are listed in Table 1.

The listings in Table 1 are somewhat different from those in the original thesis. Some changes were necessary when more recent data on Papua New Guinea languages became available. Wiru, formerly included in West Central family, is now treated as a family-level isolate. On the advice of B. Craig (Curator of Anthropology, Papua New Guinea Museum) for Ok language family, and Dr K. Franklin (Director, Summer institute of Linguistics, Ukarumpa, Papua New Guinea), for Central and West Central language families, I have re-located various members of the above families. Franklin (pers. comm.) considers that "the Kyaka area near Baiyer could well be a transitional area."

Detailed descriptions of arrows from the New Guinea mainland are rare. The only data in this context is provided by Moyne & Haddon, 1936 (Aiome people), Vicedom & Tischner, 1943–8 (Melpa speakers to the south and east of Mt Hagen), Blackwood, 1950 (Kukukuku), Van de Leeden, 1962 (Sarmi), Van Eechoud, 1962 (Kaowerawedj), Kooijman, 1962 (Star Mountains), White, 1967a (Legaiyu, Asaro), Von Wittinsburg, 1968 (Basle collection), Heider, 1970 (Dugum Dani), Clarke, 1971 (Bomagai-Angoiang), Abramson & Holst, 1973 (Hewa) and Watanabe, 1975 (West Papuan Lowland). It is not a long list and, of these, only the well-illustrated works of Vicedom & Tischner, White, Von Wittinsburg and Clarke deal with areas covered by this study. Further, these published studies have limited use for my purpose as their data do not provide the kinds of information necessary for my analyses.

I have made a distinction between primary attribution and secondary attribution to an area. I have assigned to the primary attribution category those arrows personally collected by anthropologists, patrol officers and others, who themselves have identified and documented in writing, or orally to me, the location of the arrows concerned, as well as those traditional arrows I personally collected from villages in the highlands in 1974. However, such arrows may not have been made in these villages for there exists various avenues for arrow exchange. Nonetheless, I believe that most of the arrows collected from a village, originated in or near to it.

Arrows given secondary attribution to an area are those purchased by or donated to museums as authentic New Guinea highlands arrows, and which may or may not be correctly identified and documented.

The arrows selected for study were collected before, or soon after, restricted areas were declared unrestricted, and before European contact became extensive. Pangia sub-district was declared unrestricted in 1960, and I examined H. Kerr's private collection of arrows from Borona village, in this sub-district, collected before this date. These I consider valid traditional arrows in the category of primary attribution. Another well-documented collection of arrows were those collected by D. Hoban in 1966. These are from Um sub-clan, Iore clan, Undiri census division, Mendi sub-district, Southern Highlands Divison. This sub-clan occupies land in the Mendi valley, 10 km south of Mendi township, on the south-west slopes of Mt Giluwe, at an altitude of about 1,650 m above sea-level. Such a comprehensive documentation as this is rare in ethnographic data.

Other arrows I placed in the primary attribution category were: those from the collection of S. Moriarty which contains well-documented material from many Highlands areas, including Tambul, Porgera, Keltiga, Laiagam and Tobua; and J.P. White's arrows from Lake Kopiago (Duna people). I made use of all documented arrows available at the Australian Museum (Sydney), the Macleay Museum (University of Sydney), the Institute of Anatomy (Canberra), the Papua New Guinea National Museum and Art Gallery (Port Moresby) and J.K. McCarthy Museum (Goroka). At Goroka, in 1974, the Assistant District Commissioner, N. Wilson, allowed me to examine the arrows he had

Table 1. Arrow populations studied — general summary

Language Family	No.	Documented location	Language	Owned loaned by:
Eastern	4	Upper Ramu	Gadsup	IA Can.
	8	Kambira, Gadsup Census Div.	Gadsup	IA Can.
	12	Upper Ramu	Gadsup	Aust. Mus.
	2	Gogome village	Gadsup	PNGM
	8	Yabwiara village, Aziana Census Div.	Kenata	PNGM
	3	Nire village	Gadsup	PNGM
	2	Pinata village, Upper Lamari river, Piora Census Div.	Tairora	PNGM
Total	39			
East Central	10	Legaiyu Asaro	Asaro	Aust. Mus.
	19	Otomonarche village, Unggai Census Div.	Bena Bena	Aust. Mus.
	10	Bena Bena, Bena Bena Census Div.	Bena Bena	Aust. Mus.
	3	Henganofi, Kafe Census Div.	Kamano	McCarthy Mus.
	3	Yagusa village, Kafe Census Div.	Kafe	T. Bush
	4	Lufa, Yagaria Census Div.	Yagaria	McCarthy Mus.
	5	Ya'grofa, Kamano Census Div.	Kamano	McCarthy Mus.
	1	Legaiyu, Asaro	Asaro	McCarthy Mus.
	5	Kaiyufa, Bena Bena Census Div.	Bena Bena	IA Can.
Total	60			
Central	3	Mul Council Area, Mt Hagen	Melpa	Aust. Mus
	14	Buka Pena village, Mul Council area, Mt Hagen	Melpa	Aust. Mus
	12	Yamaga village, Mt Hagen	Melpa	Aust. Mus.
	4	Mt Hagen	Melpa	Aust. Mus.
	25	Wahgi valley	Melpa	Aust. Mus.
	13	Chuave, Chimbu	Chuave	Aust. Mus.
	13	Kamul, Chimbu sub-district	Chuave	Aust. Mus.
	10	Nomane, Chimbu sub-district	Nomane	McCarthy Mus.
	6	Koge, Chimbu sub-district	Sinasina	McCarthy Mus.
	9	Koim, Mt Hagen	Melpa	McCarthy Mus.
	12	Wahgi valley	Melpa	McCarthy Mus.
	5	Nebilyer, Mt Hagen sub-district	Melpa	McCarthy Mus.
	2	Yamaga village, Mt Hagen	Melpa	McCarthy Mus.
	14	Kwip, Mt Hagen sub-district	Melpa	McCarthy Mus.
	14	Wahgi valley	Melpa	PNGM
	9	Malgi village, Mt Hagen	Melpa	PNGM
	11	Mul Council area, Mt Hagen	Melpa	PNGM
	7	Buka Pena village, Mt Hagen	Melpa	PNGM
	11	Mt Hagen	Melpa	PNGM
	11	Eltai Village, Mt Hagen	Melpa	N. Wilson, P.C.
	9	Kaip, Mt Hagen	Melpa	N. Forrest, P.C.
	9	Gumine, Chimbu	Gumine (Golin)	M. Geiua, P.C.
	7	Pari village, Kundiawa, Chimbu	Kuman	R. Simmonds, P.C.
	8	Mai village, Kundiawa, Chimbu	Kuman	R. Simmonds, P.C.
	14	Keta village, Mt Hagen	Melpa	R. Simmonds, P.C.
	7	Kenjibi village, Wahgi valley	Melpa	R. Simmonds, P.C.
	3	Kalige village, Mt hagen	Melpa	R. Simmonds, P.C.
	3	Mt Hagen	Melpa	S. Moriarty, P.C.
	11	Tambul	Gawigl (Melpa)	S. Moriarty, P.C.
Total	276			
Wiru F-L Isolate	14	Borona village, Pogoro area, Pangia sub-district Southern Highlands	Wiru	H. Kerr, P.C.
West Central	27	Iore clan, Undiri census Div. Mendi sub-district	West Kewa and Mbongu	Macleay Mus.
	22	Undiri Census Div. Mendi sib-district		D. Hoban, P.C.
	56	Lagaip river	Enga	Aust. Mus.
	11	Wabag	Enga	Aust. Mus
	3	Kyaka area, near Baiyer	Kyaka	Aust. Mus.
	6	Mendi	S. Mendi	S. Moriarty, P.C.
	4	Tobua	W. Mendi	S. Moriarty, P.C.
	16	Gadio people	Enga	S, Moriarty, P.C.
	8	Porgera	E. Ipili	S. Moriarty, P.C.
	5	Keltiga	N. Mendi	S. Moriarty, P.C.
	3	Laiagam	Enga	S. Moriarty, P.C.
	2	Iore, Mendi sub-district	W. Kewa	S. Moriarty, P.C.
	5	Mendi	S. Mendi	PNGM
	5	Kagua	E. Kewa	PNGM
	7	Tombada village, Ialibu sub-district	E. Kewa	PNGM
	10	Tari	Huli	PNGM
	6	Laiagam	Enga	PNGM
	2	Piangwanda village, Ialibu	E. Kewa	PNGM
	9	Margarima	Huli	T. Bush, P.C.

(continued on next page)

Table 1. Arrow populations studied — general summary (continued).

Language Family	No.	Documented location	Language	Owned or loaned by:
West Central	10	Sirunki	Enga	McCarthy Mus.
	5	Kwinga village, Baiyer river	Melpa	McCarthy Mus.
	7	Isale village, Ialibu sub-district	E. Kewa	N. Forrest, P.C.
	6	Rugli village, Baiyer river	Melpa	N. Forrest, P.C.
	18	Yaramanta village, Baiyer river	Melp poss. Kyaka	N. Forrest, P.C.
	5	Tobandi	Huli	N. Forrest, P.C.
	2	Gadio people	Enga	J.P. White, P.C.
Total	260			
Duna	10	Lake Kopiago	Duna	J.P. White, P.C.
	29	Lake Kopiago, Baranda Parish	Duna	Aust. Mus.
	7	Lake Kopiago, Aluni Parish	Duna	Aust. Mus.
	8	Supei clan, Giwobi village	Duna	PNGM
	8	Tumbudu river	Duna	McCarthy Mus.
	11	Kena river	Duna	McCarthy Mus.
	17	Lake Kopiago	Duna	S. Moriarty, P.C.
Total	90			
Ok	29	Telefomin	Telefol	Aust. Mus.
	21	Upper Fly river	Awin	Aust. Mus.
	14	Tifalmin	Tifal	Aust. Mus.
	8	Atbalmin	Tifal	Aust. Mus.
	1	Fegolmin	Faiwol	Aust. Mus.
	2	Woksapmin	Awin	Aust. Mus.
	14	Upper May river	Mianmin	Aust. Mus.
	6	Sogamin village	Telefol	PNGM
Total	95			
Grand Total	834			

Abbreviations.

Aust. Mus.	Australian Museum, Sydney, NSW
IA Can.	Institute of Anatomy, Canberra, Australian Capital Territory
Macleay Mus.	Macleay Museum, University of Sydney, NSW
McCarthy Mus.	J.K. McCarthy Museum, Goroka, Papua New Guinea
PNGM	National Museum & Art Gallery, Port Moresby, Papua New Guinea
P.C.	Private Collection

collected in the early 1960s from areas he had visited whilst they were still 'restricted'. Beside these, throughout the highlands I was granted many opportunities to examine smaller private collections at Mt Hagen, Kundiawa, Yagusa, Gumine, Nipa, Isale village (Ialibu) and Eltai village near Koim, south-east of Mt. Hagen.

Dates for the 'opening-up'' of areas vary considerably throughout the highlands, and before de-restriction some persons such as miners, explorers, patrol officers and linguists (usually associated with missionary work) were permitted into restricted areas. Not long after an area was declared unrestricted, European influx accelerated. Some indigenes soon realised that Europeans would trade European goods or pay cash for their artefacts, which included arrows. These consequently became a marketable asset and were manufactured for their selling potential, with makers using steel tools in place of traditional tools. Such differences as the use of 'store-paint', for filling-in or painting designs on arrows instead of traditional natural clays and ochres, and the use of newspaper, instead of bamboo or banana leaves as a padding under shaft bindings, are two of the commonest substitutions in 'modern' arrows. Whilst I was working on a collection of traditional arrows at Goroka Museum in August, 1974, a Chimbu arrow-maker approached a Museum Trustee offering to him arrows he had manufactured to sell. Technically they were expertly made, beautifully carved and coloured, but a closer examination revealed that both the above-mentioned 'innovations' had been incorporated into the manufacture of these arrows. I have avoided using such arrows in this work.

I should point out here that opportunities for innovation, and the distribution of new arrow types and designs, existed in traditional highlands societies. I. Hughes (1971) describes a network of intersecting routes, old and new, throughout the highlands (cf. Ross, 1936). Wherever trade routes existed, there was the possibility of exchange of artistic designs, either through trade or gift of the arrow itself, by picking up arrows shot by the enemy during tribal conflicts (Heider, 1970: 282; Campbell, 1937, Australian Museum Register), or by observation of elements and motifs in designs at pig feasts, *Moka* and other ceremonies where people from different clans and different linguistic units came together.

General Description of Arrow Types

Each arrow is composite in structure. It has either: (a) two component parts — a shaft into one end of which a head is socket-hafted and bound (Fig.2a); or (b) three component parts — a shaft, a fore-shaft and

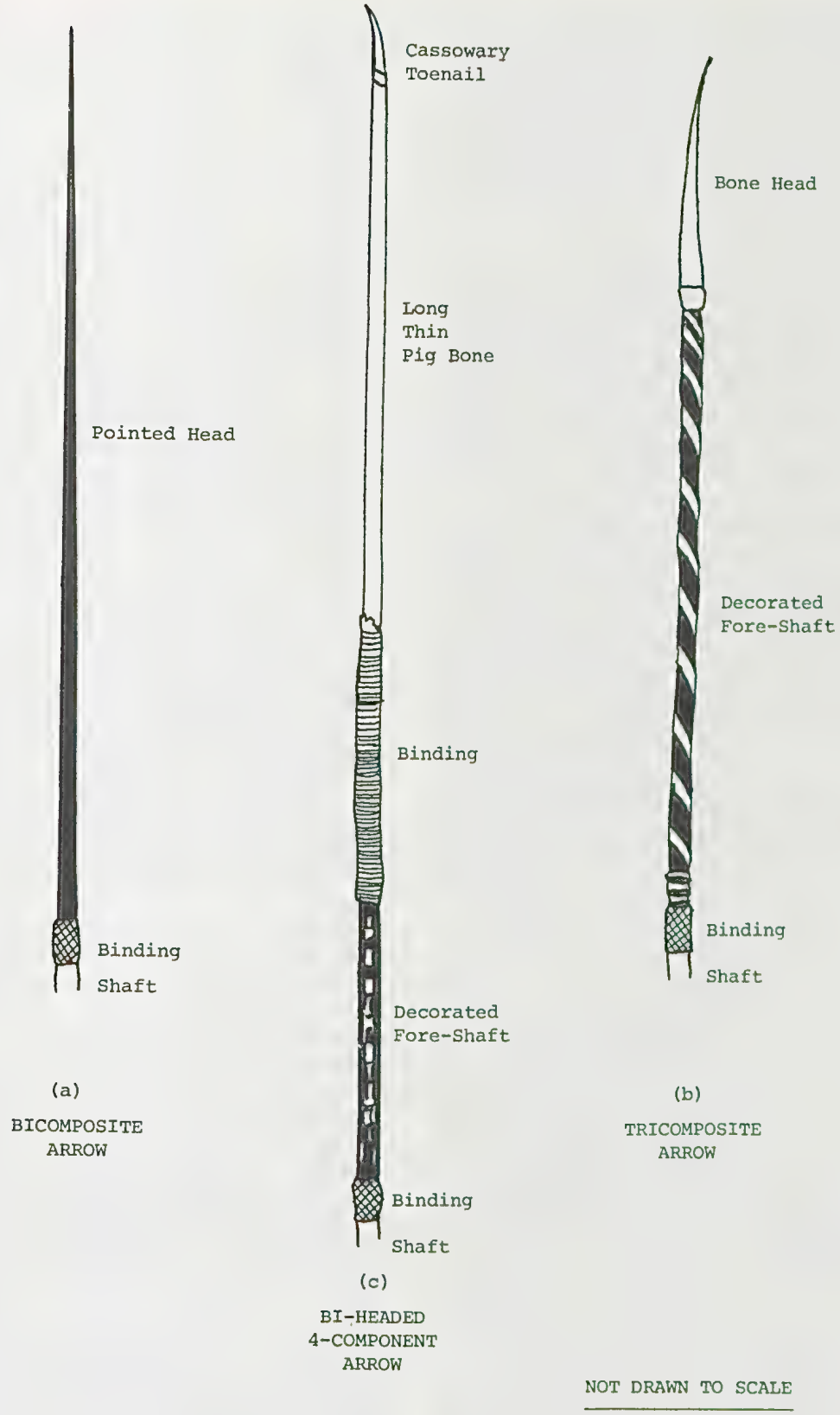


Fig. 2. Arrow types.

head (Fig.2b). The shaft is the longest part of an arrow, made from a slender reed (*Miscanthus floridulus*) a member of the same family as bamboo. The shaft varies in diameter from 0.6 cm to 1.0 cm and into one end the head or fore-shaft is hafted. The head is the distal end of an arrow, and is usually pointed. It is made either of bone, bamboo, palmwood or a hardwood. Fore-shaft is the part of an arrow that lies between the shaft and head, and is hafted to both: it is made from palmwood or hardwood.

I observed only one arrow that did not fit into the above two categories. This consisted of four parts — a normal shaft, a fore-shaft of black palmwood carved and heavily coated with red ochre, and a two-part head. The lower part was a long, thin pig-bone hafted into the fore-shaft, and on the distal end of this was hafted the pointed toe-nail of a cassowary (Fig.2c). This arrow was an extremely old, traditional type: it was part of H. Kerr's collection from Borona village (Wiru speakers).

New Guinea highlands arrow shafts have neither fletches nor nocks; they may be decorated with incised designs. Wooden heads may be decorated, but bone heads are never decorated with a carved design. Fore-shafts are sometimes undecorated, but more frequently are decorated with designs infilled and/or coloured with natural clays and ochres. These clays and ochres are sometimes treated to obtain the colour needed: pig grease mixed with charcoal (soot) to give a black pigment is common to all areas. In two regions, Pangia and Chimbu, a very rare blue subtance (vivianite) is found as nodules in river clays. This is a much desired trade item and because of its rarity is used mainly to colour designs on special arrows and ceremonial objects.

In all language family areas arrows are named according to the type of material used to manufacture their heads. Ethnographic data support the oral evidence of this trait provided to me by members of various highlands clans. As an example, I give the names used by Kewa speakers of Isale and Topopul villages in the southern part of the West Central family area:

Kone kane — an arrow with a pointed bamboo head.

Kera — an ordinary arrow with a pointed palmwood head.

Walapi — an arrow with a pointed hardwood head, often the root of a certain tree (unidentified).

Kuli — means bone in Kewa, and placed in front of this word is a qualifier that indicates the type of bone used as the arrow head.

kimbu (fibula)*kuli* (bone) — human fibula arrow head.

ali (humerus) *kuli* (bone) — human humerus arrow head.

yana (dog) *kuli* (bone) — dog bone arrow head.

mena (pig) *kuli* (bone) — pig bone arrow head.

yari (cassowary) *kuli* (bone) — cassowary bone head.

yari (cassowary) *kinbipa* (claw) — cassowary claw arrow head.

yapa kuli — is the general name for arrows when the bones of larger animals, such as the cuscus and wallaby, are used for arrow heads.

Sapula or *Walawia* — are common referral names for all famous, special arrows that have human bones for heads; for example, the bones of a leading warrior killed in battle are used for the head.

In the area covered by Iore, Ialibu and Pangia sub-districts, some arrows are carved as a series of leaves along the vertical axis of the head or fore-shaft. In Kewa language such arrows are named after the plant whose leaves are this shape (e.g. the mote plant [unidentified]) and whose wood is used for the head or fore-shafts, e.g. *mera mote* (palmwood) — palmwood head carved as mote leaves.

My chief informant, Hilary Manda Pumuye, is the son of Manda Pumuye, a specialist arrow-maker in the Pekai-Alue clan of Isale village, Ialibu sub-district. He has provided me with data regarding the use of various arrow types in his village, and a cross-check with informants from the villages of Eltai, (Hagen sub-district) and of Yagusa (Henganofi sub-district), shows all are basically in agreement, although not every arrow type was used by members of each group. Thus, arrows can be placed in generally recognized categories based on formal variations in head types which relate to differences in function.

Arrows can be classified, according to type of head, into the following categories:

1. Basic. Arrow types common to all highlands areas.

(i) Plain palmwood or hardwood head with a sharp point — common fighting arrow.

(ii) Wide, lanceolate bamboo head, with a sharp point — pig killing.

(iii) Multi-pronged head up to 14 cm long, pointed, bamboo or wood, sometimes barbed — bird or fish arrow.

2. Specific. Arrow types not present in all highlands areas.

(i) Thick, short (6–8 cm) head, blunt, for killing specific types of birds, especially birds of paradise, whose plumage and heads are used for ceremonial head-dress and as trade items.

(ii) Pointed wooden head decorated with carved design, frequently infilled or painted with natural clays and ochres and used for display at weddings, pig feasts and other ceremonies.

(iii) Tri-composite arrows: those with bones of animals or birds as heads and with carved design on fore-shafts are used for display, or for fighting special warriors, whilst those with human bones are for use against a specific person (e.g. a clan leader) or for use in a pay-back killing for a clan warrior killed in battle.

Arrow Making

In traditional New Guinea highlands societies, every man possesses his own armoury which may be self-made or purchased from arrow-makers. Among Duna men of Lake Kopiago region, about half their number make their own arrows whilst the remainder do not make any, purchasing all they require from arrow-makers (J.P. White, pers. comm.). It was indicated to me in many

highlands villages that any man requiring a special, decorated arrow for a specific purpose will have such an arrow made for him by a village arrow-maker. The carving of designs on such an arrow is the work of a specialist and technically beyond the capacity of the ordinary clansman. Though each individual is free to decorate his own collection of arrows, and some do so, the decorative art on such arrows usually demonstrates inferior technical skill.

A carved design on an arrow, using traditional stone or tooth tools, usually takes a skilled arrow-artist-decorator 4–8 hours to complete, depending on the complexity of the elements or motifs used in the design. If European steel tools are used, less time is required for carving the same design.

Descriptions of arrow manufacture in New Guinea are recorded by Blackwood (1950:42–5) and Heider (1970:282–5), but the most specific and detailed account of manufacture in the New Guinea highlands is that given by White of arrow making at Legaiyu and Batari (1967a:109–13) and by the Duna people of Lake Kopiago (1977).

Observation of Design Carving

The observations that follow were made at Isale village, Ialibu sub-district, in 1974. There I interviewed and observed the work of Manda Pumuye.

A black palm, *mera*, is usually used for arrow-heads, fore-shafts and bows, but other palms, *wame*, and *yawi*, which also grow locally, are often used. Special bows and arrows are made from *pate* or *rokopa* palmwoods which are traded from Erave or Pangia and are expensive to buy. The names of the palms are in Kewa language; I was unable to identify botanically the different species.

Arrow-head or fore-shaft manufacture at Isale begins with the felling of the chosen palm and cutting it into required lengths which are carried back to the village. Arrow-makers cut the head or fore-shaft lengths from billets of palm, shape them, and carve the designs or cut the barbs whilst the wood is still fresh.

Manda Pumuye is a specialist arrow-maker, and demonstrated to me the carving of a design on an arrow fore-shaft. The whole process took place in a sitting position on the ground outside Pumuye's house. when making an arrow he worked only 2–3 hours each day, so its manufacturing period was spread over several days. Manda Pumuye used hand-held, traditional flake tools of stone to carve his designs. These tools he called *are* as distinct from stone flakes used for general purposes which he referred to as *kana karepa*; the latter were never used for carving arrow designs as they were considered too soft ('not strong'). *Are* were obtained locally, not at a quarry site, but picked up anywhere when walking beyond the environs of his village. If they were too small to use hand-held, he hafted them into a small wooden handle.

The preparation of the surface of the fore-shaft, including its final shaping and smoothing with *nii yo* (yo = tree; the *nii* tree is a species of *Ficus*, most likely *Ficus trachypison*) leaves, took about one hour before carving of the design. The apical end was held with his left hand, the opposite end firmly fixed between his feet, and with the *are* tool in his right hand he commenced carving the design about 7.0 cms from the top. As he continued carving he slowly rotated the fore-shaft with his left hand. He seemed to work to some sort of pre-conceived design pattern, but when I asked about this, his son said he used elements and motifs as they 'come in his head'. He used some design elements (chevrons, inverted cones, concentric diamonds, zigzags) more frequently than others and, when asked why, the reason given was because his father's father and his father had used them in arrow designs.

The actual carving of the design was completed in eight working hours, and then the fore-shaft was left to dry out. Later, a bone head was to be affixed, then the fore-shaft socket-hafted to a shaft. Finally, the design was to be infilled with natural red ochre and white clay painted on with a feather. I was shown arrows with these final stages completed.

Minor differences are evidenced in some processes of manufacture; e.g. arrow-makers at Legaiyu and Lake Kopiago use *Miscanthus* for shafts as soon as it is cut and cleaned down (White, pers. comm.). In Isale village, *kapa kambe*, a species of reed cultivated for shafts of special arrows, is dried for 2–3 months before use, whereas the common reed *kambe* is used within a few days of cutting.

When the reed is dry, its outer surface is cleaned down with a hand-held stone knife, and adhering leaf-bases removed; the shaft is then smoothed with the abrasive leaves of *nii yo*.

ANALYSES

Method

I made two analyses of Highlands arrows:

1. A morphological analysis of arrow component parts — shaft, head, fore-shaft, haftings, binding type — to distinguish morphological similarities and differences so that any significant correlations can be observed and noted.

2. An iconic analysis of carved designs on arrow heads and fore-shafts, to isolate the motifs and their component elements, and determine any specific or significant combinations of these into similar designs exhibiting the same variations. This can be used to detect any patterning in relation to linguistic affinities and geographic position.

The analytic processes in this work follow, in general, those used by S.M. Mead (1968, 1971). Data relating to aspects of decoration, carving and wood used are given in Table 2.

I have concentrated on carved designs on heads and fore-shafts, but have also examined shafts of these arrows for presence or absence of decoration on them (Table 2). Time would not permit an analysis of shaft

Table 2. Comparison of decoration and arrow components by language families.

Arrows	Eastern		E. Central		Central		W. Central		Duna		Ok		Wiru	
	No.	%	No.	%	No.	%	No.	%	No.	%	No.	%	No.	%
Decorated component														
Head	25	64	54	90	196	71	84	32	48	42	39	41	—	—
Fore-shaft	14	36	6	10	80	29	176	68	52	58	56	59	14	100
Area Decorated head/fore-shaft														
Complete	11	28	11	18	80	30	103	40	60	67	48	50	12	86
Part	16	41	34	57	127	45	99	38	29	32	30	32		
2 or more than 2 separate areas	12	31	15	25	69	25	58	22	1	1	17	18	2	14
Motif numbers used														
1 motif	27	69	51	85	177	64	162	62	63	70	67	70	4	28
>1 motifs	12	31	9	15	99	36	98	38	27	30	28	30	10	72
Type of Carving														
Deep	8	21	14	23	137	50	158	61	60	67	70	74	13	93
Medium	13	33	36	60	125	45	92	35	26	29	21	22	1	7
Light	18	46	10	17	14	5	10	4	4	4	4	4		
Wood type Used														
Palm	30	77	40	67	193	70	160	62	66	73	71	75	10	72
Hardwood	9	23	20	33	83	30	100	38	24	27	24	25	4	28
Shaft														
Decorated	11	29	32	54	113	41	71	27	20	22	64	67		
Undecorated	28	71	28	46	163	59	189	73	70	78	31	33	14	100
Total Number Examined for each Family	39		60		276		260		90		95		14	

decorations, so I made a selection of basic types of shaft designs which provide sufficient data to give some idea of the pattern of their distribution.

The shaft diameters of all arrows examined were measured, but variation was so minimal that I suggest it is the result of environmental factors affecting the growth of the plant used (*Miscanthus floridulus*) within a particular region, and not a specific choice made by the arrow-maker himself.

I have not attempted to analyse the multiplicity of barbing styles, but where an arrow head exhibits a carved design in addition to barbs, the design pattern has been included (Figs 32, 33).

I have made three assumptions:

1. That a design carved on any single arrow is the work of one man only. This assumption is based on data supplied by J.P. White (1967a), oral evidence from arrow-makers, and personal observations of arrow manufacture in Yagusa village (Henganofi sub-district, Kafe dialect speakers) and Isale village (Ialibu sub-district, Kewa speakers).

2. That arrows documented from a location were in fact manufactured in the specific location indicated — the named village, or from within a local district.

3. That the change in technology, from the use of stone and/or tooth to steel, has not caused any change in design elements, motifs or patterns that are observable as decorative art on New Guinea highlands arrows.

Morphological Analysis

Shaft decoration. Arrow shafts can be categorized into two groups: (I) decorated and (II) undecorated. The presence or absence of shaft decoration throughout the highlands is a regional characteristic; e.g. in the southern part of West Central family area (Mendi, Ialibu, Nipa etc.) shaft decoration is completely absent, whilst in the northern part (Wabag, Porgera) shafts are decorated.

If we include as decoration the removal from the shaft of axial strips of epidermis, then we can indicate two decorative types (A) and (B), with (B) having one variable in technique (Figs 3 & 4).

Type I (A): where the epidermis is removed as noted above, seen on shafts from East Central (Bena Bena), Central (Wahgi valley), and the northern part of West Central (Porgera) family areas. The strips removed are approximately 2 mm wide and may be long or short, commencing at a node and sometimes extending the full length of the internode. This form of decorative art is rarely used on any other artefact.

Type I (B): lightly incised designs, almost scratches, made with a very fine tool. Circles, zigzags, triangles, crossed lines and ellipses are elements used on some shafts in most highlands areas.

Type I (B)i: this variation in shaft decoration uses an additive technique: the designs are made more positive by rubbing over them with blackened wax (e.g at Bena Bena and Karimui).

Types (A) and (B) are sometimes both present on the same shaft in the East Central, Central and Duna family areas.

Many Bena Bena arrows exhibit a shaft decoration (Fig. 3 a, b), referred to as the 'running s', that I did not find used on arrow shafts from other areas of the highlands. It is present elsewhere in New Guinea, in designs on other artefacts: painted on shields of the Asmat (Rockefeller, 1961), etched on bamboo in north-east New Guinea (Bodrogi, 1961) and on sago spathes of the Awai (Newton, 1967). Within the New Guinea highlands its use is seemingly confined to arrow shafts in one area within East Central family boundary.

Hafting. In this context 'hafting' refers to the manner in which component parts are fixed together to make a complete arrow. Hafting techniques employed by New Guinea highlanders vary directly with the different manufacturing materials used, and position of parts needing to be hafted.

Three types of hafting techniques were observed:

1. Socket hafting. In all arrows where hafting was

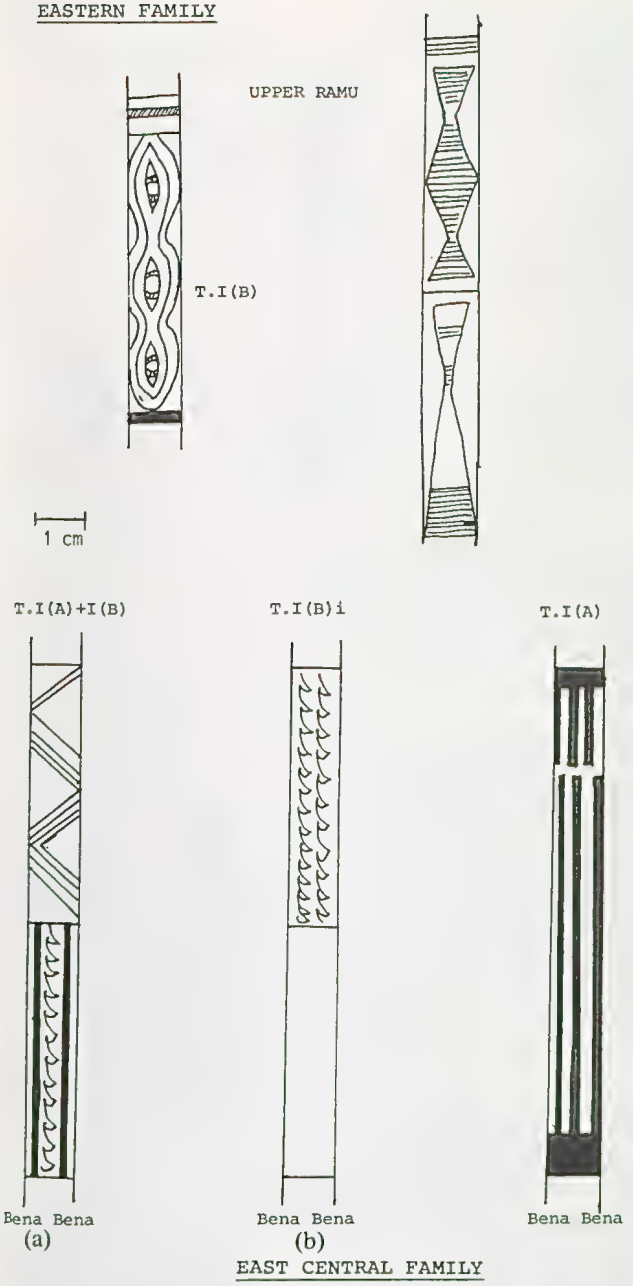


Fig. 3. Shaft decoration.

discernible, the head or fore-shaft is tapered and socket-hafted into the central hollow of the shaft. This is the only method described by Blackwood (1950), Heider (1970), Moyne & Haddon (1936), White (1967a), and is what I saw at Yagusa village. Two types exist: (i) fore-saft or head into hollow of shaft (Fig. 5.1a); (ii) fore-shaft into head. When the head is hollow animal bone, the wooden fore-shaft is thinned and socket-hafted into the bone cavity (Fig. 5.1b).

2. Surface laid to surface. When head is a long bird bone or talon, thin pig bone or lanceolate, flat bamboo, the proximal end is laid flat against the free end of the fore-shaft, overlapping a certain distance, then bound in this position (Fig. 5.2).

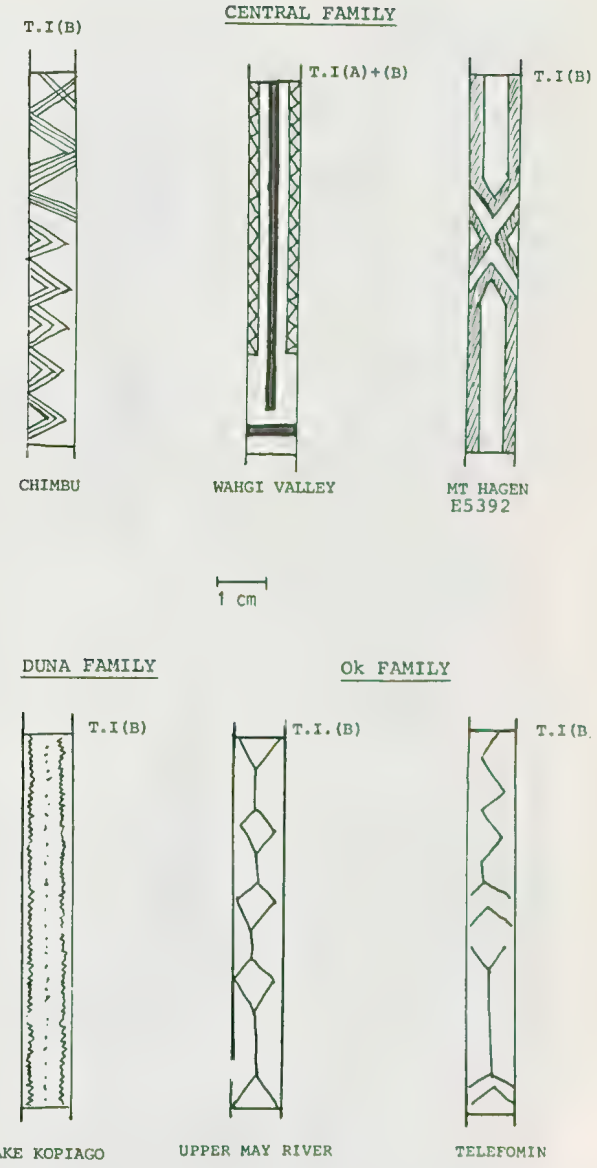


Fig. 4. Shaft decoration.

3. Hafting into split fore-shaft. an alternative method for hafting the same head types as (2) above. The fore-shaft free end is longitudinally split a suitable distance and sometimes enlarged, and the head is inserted into this split, and bound (Fig. 5.3).

These three types are present in all areas and there was no evidence of variation in their distribution.

Additives used in hafting. All types of bindings, insect wax, tree resins and natural clays I consider additives to haftings. In all arrows the shaft hafting area was bound with one of the three types of bindings described below, and in some, wax or resin was used as a fixative, and sometimes rubbed into the binding. Insect wax mixed with soot is the most commonly used; it sets hard and can be mistaken for pitch. This wax comes from a type of bee (not the honey-bee) called *enko* in Wiru language, while resin is from the *pangeo* tree (H. Kerr, pers. comm.).

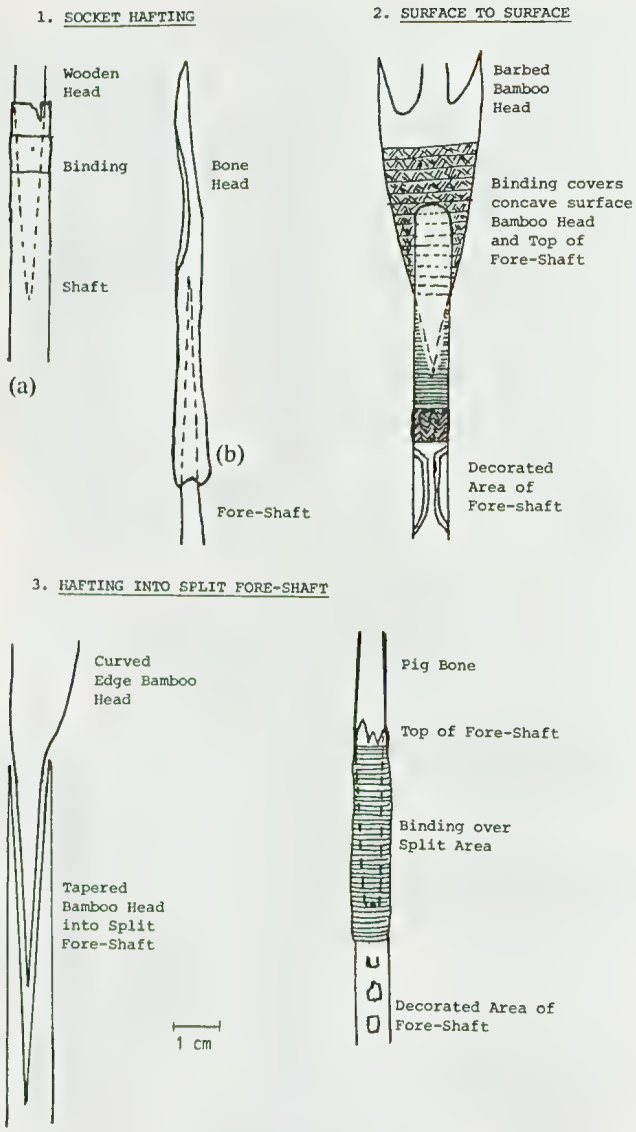


Fig. 5. Hafting types

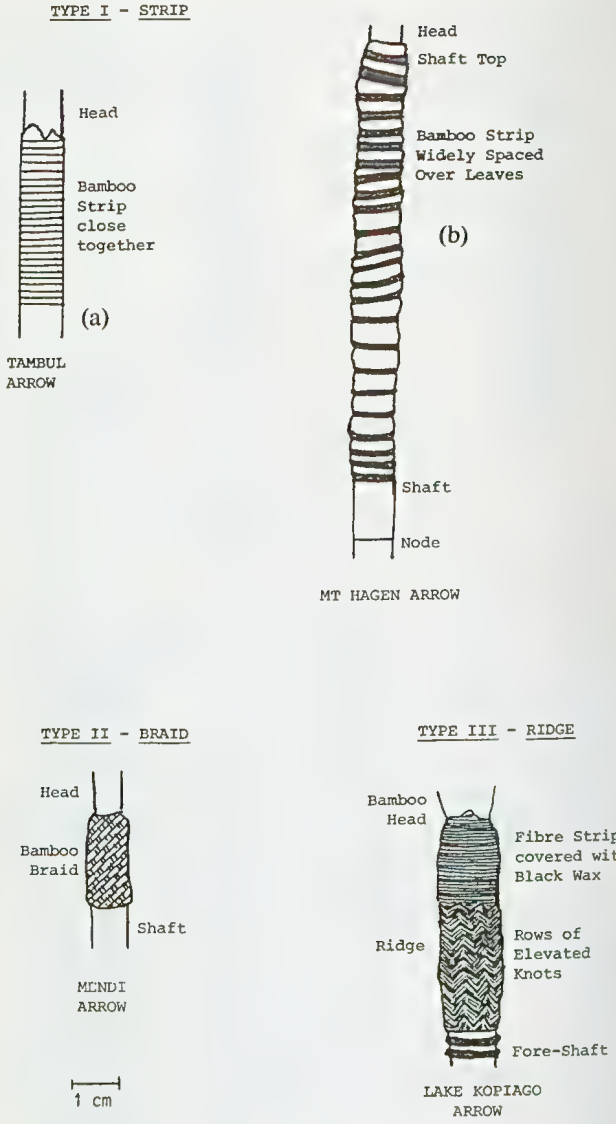


Fig. 6. Binding types.

Binding types. Three types of binding material were used: (i) long, narrow (1.0–1.5 mm in width), flat strips of the epidermis of a bamboo with extremely long internodes; (ii) epidermis of orchid petiole in similar strips; (iii) fibres made from the inner bark of various trees growing in specific areas: *Gnetum gnemon*, *Maoutia* sp., *Broussonetia papyrifera* (paper mulberry). After treatment, usually by rolling with the palm of the hand against the bare thigh, the bark looks like fine twine which is used for binding and other purposes.

The choice of material for binding is probably simply a reflection of what suitable material is available, which is determined by climate and other physical factors, and also trade. For instance, the species of *Dendrobium* orchid whose epidermis is used for coloured strip and braid binding grows in high altitude forest but is traded to other areas.

I observed only three types of binding techniques used for securing hafted arrow parts. For one, I have adopted the term used by Heider (1970), braid binding. Ethnographic records describe, but do not provide names for, the other two, so I used my own terminology, based on their appearance. The distribution of binding types and materials by language family is given in Table 3.

1. Strip binding. The binding material is wound in a spiral mode around an arrow part so that each circumferential turn very closely approaches the one adjacent to it (Fig. 6a). When a padding of leaves of reed, banana or bamboo is used underneath, the turns are spaced further apart (Fig. 6b). This is, in fact, a double binding type, for underneath the padding the area has already been bound with close strip binding. Its use seems confined to East Central and Central family arrows. Bamboo strip is always used on such doubly-bound arrows. Coloured orchid petiole is also commonly used to bind arrows from East Central and Central family areas.

Table 3. Distribution of binding types and materials by language family.

Languague Family	Bamboo Strip	Strip over Leaves	Coloured Orchid Strip	Orchid Fibre Strip	Woven Braid Fibre Strip	Bamboo Braid	Coloured Orchid Braid	Ridge
Eastern	★		★	★	★	★	★	
East Central	★	★	★			★	★	★
Central	★	★	★	★		★		★
West Central	★			★		★		★
Wiru	★			★		★		
Duna				★		★		★
Ok	★		★	★	★	★		★

Bark fibres, too, may be used for simple strip binding, mainly on arrows where a bamboo head is hafted to the fore-shaft. The binding is often covered with blackened wax or clay. This is seen on arrows from Central family area and all areas to the west.

The use of plaited fibre for strip binding to haft bamboo heads to fore-shafts was found in only two areas: Upper Ramu, Eastern family, (one arrow); and Ok family (nine arrows). Sometimes this binding was cross-lashed over ordinary fibre strip to give added security to the hafted parts.

Strip binding in its various forms is in common use throughout the Highlands.

2. Braid binding. This consists of closely plaited strips of either bamboo or orchid epidermis. It is universally used throughout the highlands except on Duna family arrows (Fig. 6).

3. Ridge binding. This is closely woven. It is similar to braid binding but at intervals the braid is knotted when woven, producing regular ridges of 'elevated knots' vertically disposed in close linear succession throughout the binding area. This results in a symmetrical (uniform) succession of vertical ridges (elevated knots) and depressions (flat braid) in the binding pattern (Fig. 6).

This binding method is not used in many areas but is widely used in some, especially on Duna and Ok family arrows; it is used in the northern part (Porgera) of West Central family area but is totally absent in the south. The people of Legaiyu, Asaro, (East Central family) frequently use this binding type, and it was seen on a few arrows from Tambul and Mia river, (Central family area).

Technologically these three binding types might be placed along a continuum from simple to complex, with strip binding at the simple end, ridge binding at the complex end and braid binding half-way between, but whether highlanders regard them in this perspective was difficult to ascertain. At Isale village, where ridge binding is never used, I was told that it was 'very difficult'. In general, however, binding on arrows seems to be a mechanical process, the binding type used being the one at which the craftsman is most adept.

Length of arrows. The overall length of all arrows from each language area was measured to investigate the apparently significant differences in length. This analysis was carried out under the guidance of Professor R.V.S. Wright, Department of Anthropology, University of Sydney. The findings are summarized in Table 4.

Table 4. Length of arrows from different language family areas. Lengths are in cm. $\bar{x}$ = mean; s = standard deviation; N = number of samples. Newman-Keuls results are explained in the text.

Name of Family	Newman-Keuls	N	$\bar{x}$	s
West Central	c	260	115.61	7.88
Duna	c	90	115.85	8.50
Central	c	276	120.75	11.68
Wiru	bc	14	122.20	5.01
Eastern	bc	39	123.83	15.75
East Central	bc	60	123.83	11.76
Aiome	bc	10	124.35	2.39
Karimui	b	14	129.47	3.21
Ok	a	95	142.95	12.08

These results were tested and further analysed by Professor Wright, who has provided the following discussion of his results:

"A one-way analysis of variance confirms what is obvious from inspection of the means, namely that there are some significant differences between them. I have applied, as a more penetrating analysis, the Newman-Keuls test for sequential testing of means (Snedecor & Cochran, 1967:273). This test allows one to examine each group and decide from which of the rest it is significantly different. The results of the Newman-Keuls test are presented by means of the letters in Table 4. A group is significantly different from another group if the two do not share at least one common letter. Thus we see that at the 0.05 level of probability Ok is significantly different from all the other groups and that Karimui is significantly different from West Central, Duna and Central, as well as from Ok."

Within each language family area, I found that the lengths of arrows were normally distributed about the mean (Table 4). It might be expected that, where arrows were made by specialists, there would be greater uniformity in lengths compared to situations in which each person made his own. Some hint that this might be so is given by the low range of lengths of arrows from Duna and Wiru families, but data on makers of individual arrows in my samples are insufficient for proper assessment.

Heads and fore-shafts. With regard to fore-shaft function the only conclusion I could reach is that arrows with decorated fore-shafts are more highly prized than those with decorated heads, for purely aesthetic reasons and they give added prestige to their owner. It seems

that, as projectile weapons, arrows with fore-shafts are no more deadly or accurate in flight than those without. This was demonstrated to me at Yagusa village so I would say fore-shafts are unimportant structurally but important as design fields on which highlanders can display their artistic talents. Fore-shafts thus have a role in the culture of the clan.

In all areas under study arrows with fore-shafts were present (Table 2) and display certain traits:

1. When heads are of bone this attached to a fore-shaft;
2. When heads are of bamboo and attached to a fore-shaft, this fore-shaft is much shorter in length than when the head is bone;
3. Certain arrow types always have fore-shafts and are always well-decorated.
   (a) special arrows for display at ceremonies such as *Moka* and pig feasts;
   (b) arrows used by famous clan warriors in fights;
   (c) arrows used by kin in pay-back killings: this is probably because all such arrows have bone heads, usually those of the slain person whose death is being avenged.

Fore-shafts of arrows with bone heads are always decorated with carved designs in the West Central family area, whilst those with bamboo heads are rarely decorated. In other family areas to the west, particularly Duna and Ok, fore-shafts are elaborately decorated whether heads are bone or bamboo. In these two areas, fore-shafts are much shorter and thicker than those of family areas eastwards, especially when bone heads are used. West Central family arrows have long, slender fore-shafts.

With the exception of Eastern family area, all barbed arrows from the study area exhibit a short design on the head next to the shaft. Simplicity in design is achieved by the use of one element only — circles in Eastern and East Central family areas, occupying only part, never the complete area, of head or fore-shaft; and spirals in West Central area (especially the southern part), covering the whole head or fore-shaft.

Discussion. Figure 7 shows the ratio of all decorated fore-shafts to all decorated heads in each of the language family areas. A change is noted between eastern areas and those to the west. The area of change appears to be between Central and West Central family areas; in the east, arrow heads are more frequently decorated than fore-shafts, whilst in the west the opposite occurs.

The data in Table 2 concerining area of heads and of fore-shafts decorated also show a geographic trend. If the various possibilities are listed according to frequency (Table 5), then it becomes apparent that there is a difference between east and west areas, the transition zone being Central family area. This was confirmed by a chi-square test, which showed a significant difference between east and west areas.

The data in Table 2 (use of more than one motif to form a design pattern) indicate that the use of one motif is preferred in all areas except Wiru.

Table 2 also examines depth of carving. Definitions

Table 5. Area of head or fore-shaft decorated — summary. a = completely decorated; b = partly decorated; c = 2 or more areas of decoration.

	Eastern	East Central	West Central	West Central	Duna	Ok
Most common	b	b	b	a	a	a
Next common	c	c	a	b	b	b
Least common	a	a	c	c	c	c

used are: deep, design cut 1.5–2.5 mm deep into surface area; medium, design cut into surface to a depth of 1.0 mm; light, design lightly incised or scratched on surface — depth not measurable. The depth of carving designs could be placed along a continuum starting with lightly incised in Eastern family area, mostly medium deep in East Central, medium and deep used almost exclusively in Central, with deep carving the major type in families to the west (Table 6).

Table 6. Depth of carving — summary. a = deep, b = medium, c = light.

	Eastern	East Central	West Central	West Central	Duna	Ok
Most common	c	b	a	a	a	a
Next common	b	a	b	b	b	b
Least common	a	c	c	c	c	c

The frequency tabulation suggests a division between East and West with Central as the transition zone. This was confirmed by a chi-square test.

Type of wood used (Table 2) is not a useful indicator for differences, because this depends on wood types available locally or whether a person is sufficiently wealthy to buy or exchange goods for the more prestigous palmwood.

The data in Table 2, concerning shaft decoration, do not furnish evidence for a transition zone between east and west.

Table 3, distribution of binding types and materials, indicates arrows of West Central, Wiru and Duna families use fewer — 3 or 4 out of 8 — of the possible combinations than arrows of language families to the east, where 6 or 7 of the 8 combinations are used.

It is evident from the morphological analysis that:

(a) the tradition of carving designs on arrow heads and fore-shafts is universal throughout the Highlands;

(b) the Chimbu-Asaro Divide is less of a barrier to arrow form and design than was expected;

(c) there is evidence for an east–west dichotomy, the boundary of which seems to correspond for the most part to the Central–West Central language boundary, from the Yuat river in the north through Mt Hagen area to the Kaugel river in the south. Central, East Central and Eastern language areas lie to the east of this; West Central, Duna and Ok to the west;

(d) the data point to Central language family area as a transition zone between east and west. I checked to see if the changes could be clinal due to differences in settlement time-depth (as derived from archaeological data), but the results proved negative.

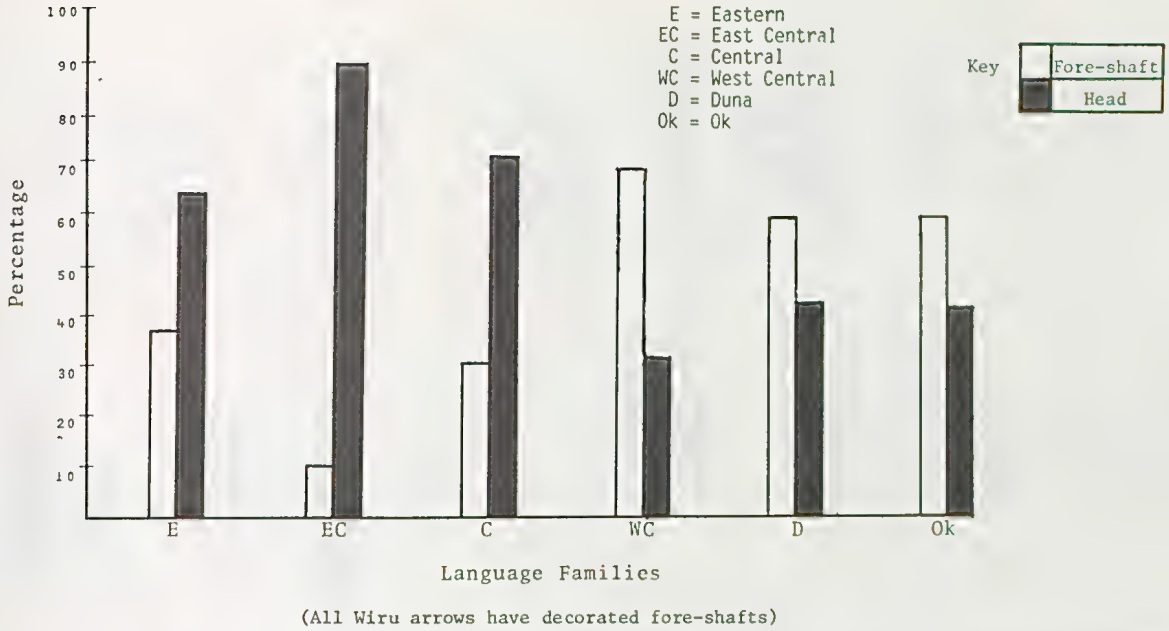


Fig. 7. Ratio of decorated head to decorated fore-shafts, by language family (all Wiru arrows have decorated fore-shafts).

Iconic Analysis

Before proceeding to an iconic analysis of elements and motifs in design patterns, it is necessary to clarify the meaning of terms used.

A design element is the fundamental unit of design. An element may be used by itself in a design, or it may be used in combination with other elements to form motifs in design patterns.

A motif can be formed from one element repeated, or from a combination of two or more elements. The only design elements on arrows considered in this investigation are those carved or incised on arrow heads or fore-shafts. They may or may not be infilled or painted with coloured clays and/or ochres.

The design field is that area of the head or fore-shaft used by the artist to display a carved design.

A boundary marker is usually a simple element, such as a circle, that marks the upper and lower limits of a complete design.

In comparison to other material objects (such as shields, masks, and house-boards) on which the New Guinea Highlanders display their artistic talents, the design field available to the arrow-carver is very limited. Its extent depends entirely on the length of arrow heads and fore-shafts, and the shape of their surfaces. Although the majority are more or less round in cross-section, oval shapes also occur, and these two types provide an elongated and curved surface for the carver. Triangular and rectangular-shaped heads occur in some arrows, especially those where the upper part is barbed above the carved design area, and provide an elongated flat and angular surface. The restricted design fields must place constraints on the types of elements and motifs the arrow artist can use. In addition, the few types of manufacturing material available — wood from various species of palm (*Oriana, Licuala*, black palm indigenous to an area or traded from elsewhere) or hardwood (unidentified) — must place further limits on his artistic representations.

Boundary markers are almost completely absent from arrow designs. Their rare use at the end(s) of designs seems to be simply personal choice.

Element Codification. Within the confines of this study it has not been possible to isolate every element used in arrow designs throughout the highlands. Each element indicated has been selected on one of two criteria: (i) the frequency of its occurrence; (ii) its restriction to certain areas.

Whether an element's position is around or along the vertical axis of arrow heads or of fore-shafts, it is treated in the same body of data, but its position is identified by either drawn lines or notes. All elements are illustrated with the arrow head upwards. Shading indicates intact wood, with unshaded areas indicating carved-out parts.

ELEMENT 1: circle (Fig. 8)

(i) lightly incised around head or fore-shaft

(ii) deeply carved around head or fore-shaft

ELEMENT 2: diamond (Fig. 8)

(i) lightly incised

(ii) centre solid with deep incision surrounding it

(iii) centre deply hollowed-out, an 'empty' 'eye'

(iv) deeply incised with centre left solid

(v) centre a small hollow in a solid diamond shape

[(ii)–(v) are termed 'ocular' or 'eye' variants]

ELEMENT 3: triangle (Fig. 8)

Rarely used in singular form, but is the basis of duplicate forms and single motifs made up of this one element.

(i) lightly incised; often occurs as concentric triangles in either vertical or horizontal postion

(ii) deeply carved, solid; notches along the vertical axis

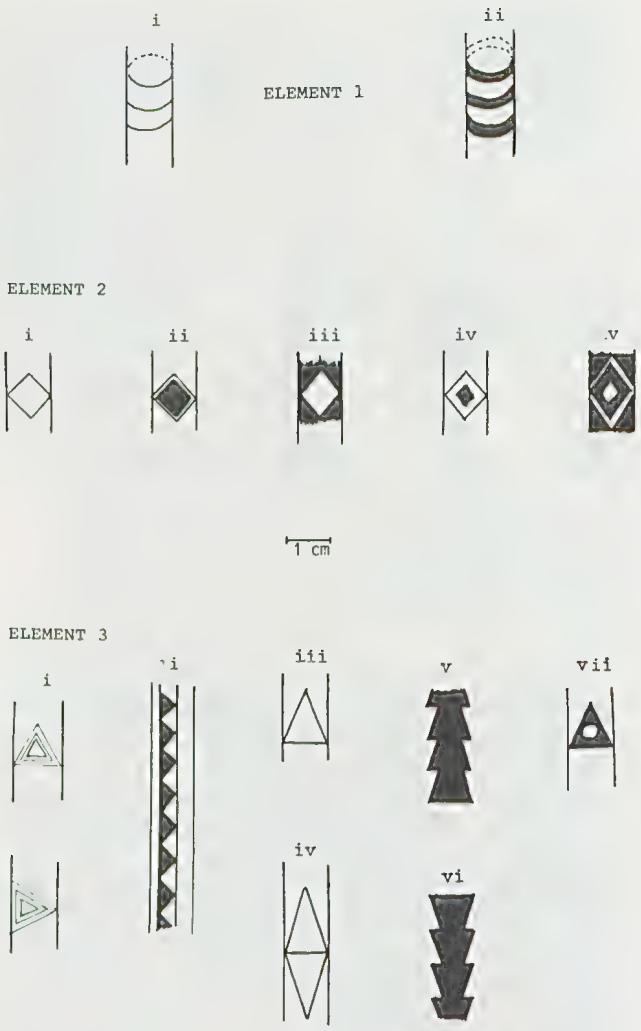


Fig. 8. Variants of elements 1, 2 and 3.

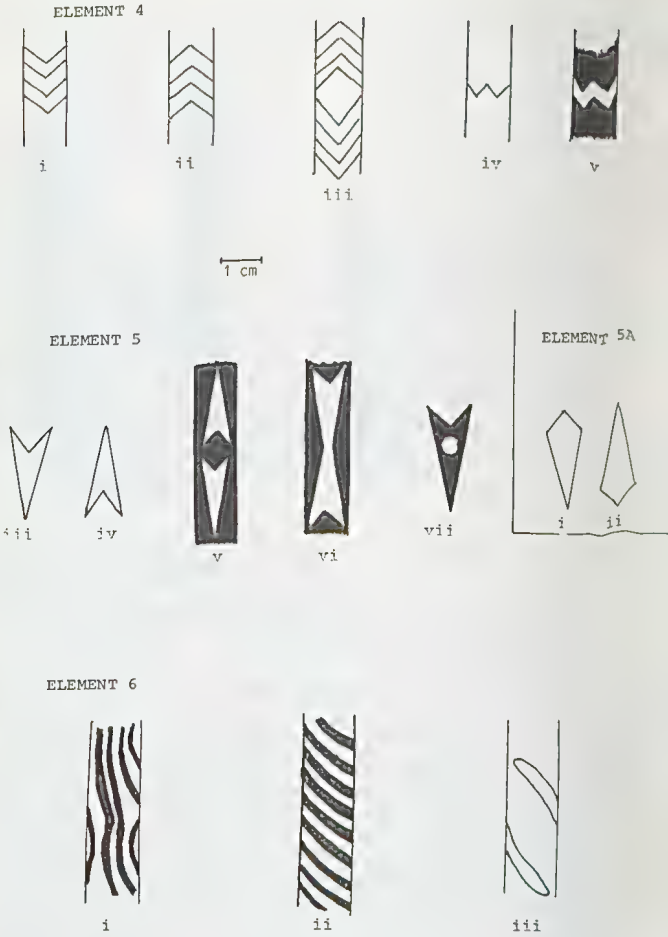


Fig. 9. Variants of elements 4, 5, 5A and 6.

in singular progression

(iii) centre deeply hollowed-out

(iv) two triangles sharing one base-line, deeply hollowed out, in vertical position

(v) carved in vertical linear series with apical angle of each succeeding lower triangle cut off by base-line of adjacent upper one producing an 'inverted cones' effect

(vi) same as (v) but inverted

(vii) solid triangle with hollowed-out circle in centre

ELEMENT 4: chevron or zigzag (Fig. 9)

As chevron it is rarely used in singular form. Variants (i)-(iii) are usually lightly incised.

(i) chevrons in vertical linear succession

(ii) chevrons inverted in linear succession

(iii) chevrons in opposition

(iv) zigzag lightly incised around vertical axis

(v) zigzag deeply carved around vertical axis

ELEMENT 5: four-sided figure (Fig. 9)

Two long sides meet in acute angle, 2 short sides re-entrant.

(iii) short sides re-entrant, lightly or deeply carved

(iv) as (iii) but inverted

(v) = (iii) + (iv) in opposition, deeply incised

(vi) = (iii) + (iv) joined at tapered end with no interruption, deeply carved

(vii) a solid form of (iii) with deeply hollowed-out circle at its wide end

ELEMENT 5A: similar figure with 2 short sides everted (Fig. 9)

(i) short sides everted, lightly or deeply incised

(ii) as (i) but inverted

ELEMENT 6: spiral (Fig. 9)

All deeply carved.

(i) loose vertical spiral that does not completely encircle the head or fore-shaft with each turn

(ii) spiral making complete turns around the vertical axis

(iii) an S-shaped spiral that makes only one complete turn around vertical axis.

ELEMENT 7: shield (Fig. 10)

(i) centre hollowed-out

(ii) deeply hollowed-out except for cigar-shaped centre which is grooved horizontally

(iii) whole centre left solid except for horizontal grooves

Fig. 10. Variants of elements 7, 8, 9 and 10.

(iv) broader in outline, deeply carved, with solid areas left in a vertical line in the centre

ELEMENT 8: lanceolate, leaf-like shape (Fig. 10)

(i) in vertical linear succession

(ii) smaller, double leaf-shape around the vertical axis

ELEMENT 9: shape similar to element 5 (iii) but with long sides curved (Fig. 10)

(i) centre deeply hollowed-out

(ii) centre hollowed-out except for an elongated solid area

(iii) same as (ii) but a row of separated solid areas in centre

(iv) heart-shaped with centre deeply carved out

ELEMENT 10: hourglass shape (Fig. 10)

(i) curved ends indented to form V-shape

(ii) part of head or fore-shaft carved into this shape

ELEMENT 11: six-sided rectilinear figure (Fig. 11)

Two long sides are parallel and 4 short sides everted.

(iii) short sides everted, parallel sides elongated.

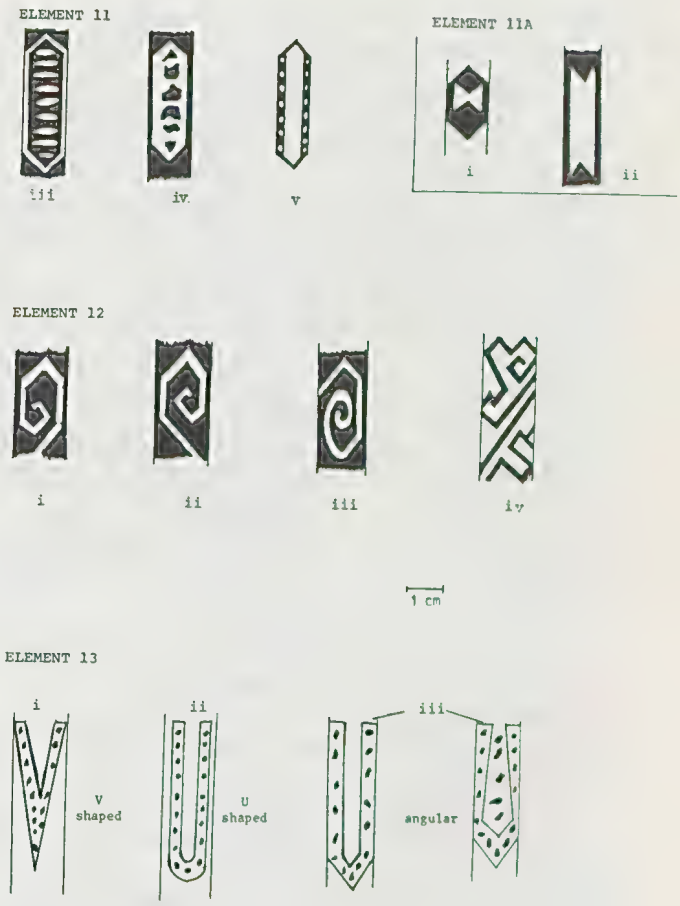


Fig. 11. Variants of elements 11, 11A, 12 and 13.

Centre solid, cut by several grooves

(iv) same as (iii) but centre is carved out except for a row of solid areas down the middle

(v) same as (iii) but centre is carved out and outer rim is cut by small grooves

ELEMENT 11A: similar 6-sided figure with each pair of short sides re-entrant (Fig. 11)

(i) centre deeply carved, parallel sides short

(ii) same as (i) except parallel sides are elongated

ELEMENT 12: geometric figure (Fig. 11)

Deeply carved, often continues around head or fore-shaft, but frequently used as part of a vertically placed motif.

(i) geometric, angular, spiral, vertical position

(ii) mirror image of (i)

(iii) elongated, geometric spiral whose internal sides tend to be somewhat curved

(iv) complicated geometric angular form that continues around head or fore-shaft, deeply carved

ELEMENT 13: grooved element (Fig. 11)

(i) groove with pointed end — V-shaped

(ii) groove with straight sides and rounded end — U-shaped

(iii) groove with sides straight or angled, with an angular pointed end

Grooves sometimes contain a line of solid dots carved within or around the groove. Where this occurs I shall

indicate their occurrences by writing '(dots inside)' for the former, and '(dots outside)' for the latter.

Analytical Procedure. I took each of the 13 elements in turn and using all 834 arrows, but keeping them in their respective language family groups, investigated the way these elements were combined and positioned in design patterns. A summary of my findings and selected arrows to illustrate points in this summary are presented. In my use of the terms 'upper' and 'lower', I am referring respectively to those parts of the arrow head or fore-shaft furthest away from, and nearest to, the shaft; 'at the shaft' means the design commenced where the head or fore-shaft is hafted to the shaft, whilst 'near the shaft' indicates the design commences about 1–4 cm above this hafting area. Within the design area, 'upper' refers to that part of a motif or design nearest the distal end, 'lower' to that part nearest the shaft.

On the accompanying tables I have indicated the positioning of elements and the position of each variant, as being:

(a) in the centre of design;

(b) as part of upper motif, or (bi) part of lower motif;

(c) at upper end, or (ci) lower end of design — boundary markers;

(d) as the complete upper motif, or (di) complete lower motif;

(e) as the only element used in the design.

I have indicated the number of occurrences of each variant of each element in design patterns on Table 7, positions of element variants and the number of arrows on which they occurred in each position on Table 8, the distribution of design elements by language family in Table 9, and the positioning of each element in design patterns on Table 10.

In Figs 12–33 (element variants in design patterns), elements other than the one referred to in the figure caption are identified in full, for example, (E_v4) means Element 4 variant (v).

ELEMENT 1: circles

Eastern and East Central family areas. Here circles most frequently occur in several groups along the arrow head or fore-shaft with lightly incised diagonal lines between them (Fig. 12a). Circle groups are separated by undecorated areas and never begin at the shaft. Often one or two medium-deeply carved circles are found at the lower end of these groups (Fig. 12a,d). Colour is not widely used on designs in these two family areas, but some Eastern area arrows have red ochre rubbed along the head length or over incised circles, whilst some Bena Bena (East Central) arrows have red ochre on undecorated areas between circles.

Central family area. On arrows from this area, circles are never used singly, always in pairs or as a series of circles repeated as the other motif is repeated along the design area (Fig. 13a). Usually a white clay infill is used.

West Central family area. In the northern part of this area, circles are infilled alternately with red and white ochre/clay, and are never used singly. Most favoured are groups of three, four or five, separated by short

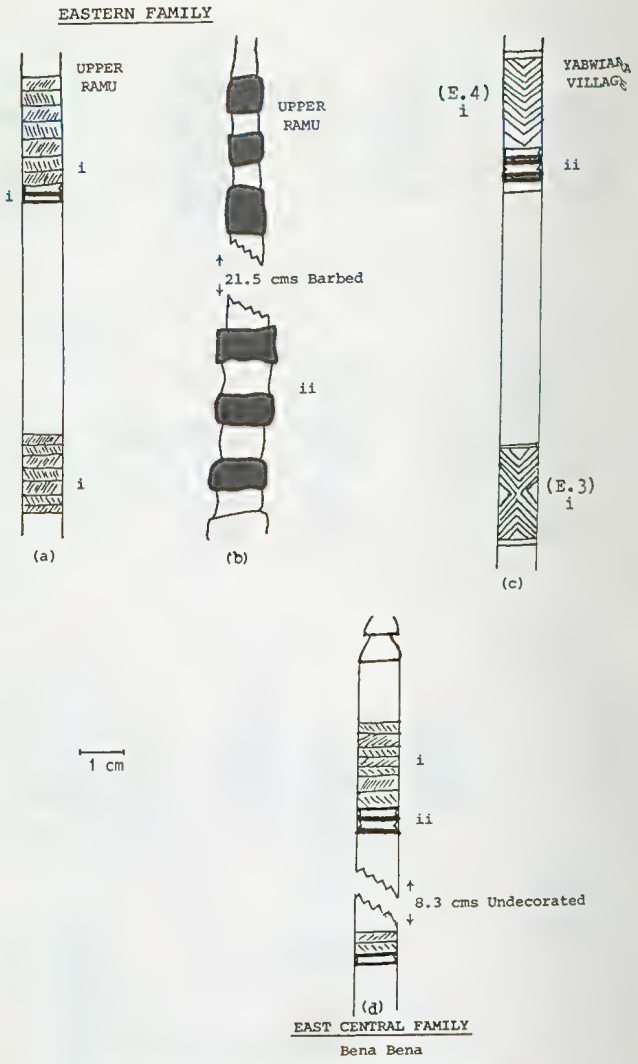


Fig. 12. Element 1 variants in design patterns.

undecorated areas. In the southern part, where approximately 75% of arrow designs use circles, they are used mostly in threes or fours as an integral part of the complete design. On some Mendi arrows (Fig. 13b) circles only are used as the upper half of a two-motif design carved above an area of small barbs at the shaft. Red, white, orange and yellow ochres and clays are used to colour designs.

Wiru family-level isolate area. In this area circles area sometimes used as boundary markers to enclose the design.

Duna family area. The use of circles in a design pattern on arrows from this area may depend on the width of the head or fore-shaft. The only arrows I examined from this area that had several circles in the design were ones with long thin heads, where circles were used in twos or threes, often to separate motifs in the design. All were deeply carved with red or white infill. On lavishly decorated fore-shafts of Lake Kopiago arrows (Fig. 13d) very deeply carved circles are used with alternating red and white infill.

Ok family area. In this area when barbing occurs on

Table 7. Frequency of occurence of variants of elements, by language family.

No. of arrows	Language Family	El.1 Var.		Element 2 Variants					Element 3 Variants							Element 4 Variants					Element 5 & 5A Variants							El.6 Var.		
		i	ii	i	ii	iii	iv	v	i	ii	iii	iv	v	vi	vii	i	ii	iii	iv	v	i	ii	iii	iv	v	vi	vii	i	ii	iii
39	E	225	56	8	8				4								20	28	23										7	
60	EC	293	73		8				5								17	24	33	14									10	
276	C	357	331	108			245		82		70					40	41	72	84	154							6		4	
260	WC	218	248	15		63	199	68	12	27	120	117	45	31	22	27	27	74	56	116	66	69			36	35		8	58	
90	D		280		28	76	42		27	67			22			6						25		31						7
95	Ok		167	10	8	61	16		36				10	7				10		94	30	36	13	25	4	37				
14	W		9			6		21	14		32	6	7		14					36										

No. of arrows	Language Family	Element 7 Variants				El.8 Var.		Element 9 Variants				El.10 Var.		Elements 11 & 11A Variants					Elements 12 Variants				Element 13 Variants		
		i	ii	iii	iv	i	ii	i	ii	iii	iv	i	ii	i	ii	iii	iv	v	i	ii	iii	iv	i	ii	iii
39	E	4																							4
60	EC																								
276	C																								
260	WC		38	12	54	10		40	28	19	183	10	9			75	96	30	12	13				9	34
90	D		7					5									39						38	15	
95	Ok				9	3		25	9	5	70			21	10		2		4	20	6	7	17	15	8
14	W	2	4		12	43	18					32					12	8							

heads, circles seem to be used as a way of separating the design from the barbed area. Some Telefomin designs use circles this way, but in others, circles are absent. No circles are used in designs on Tifalmin arrows, whilst on Upper Fly and Atbalmin arrows they are used only as boundary markers. When present almost all are coloured red and white (Fig. 20c, d).

Comments on use of Element 1. Five arrows were anomalous in their use of Element 1. Two arrows from Upper Ramu (Eastern family) used variant (ii), elongated and so deeply carved as to be almost notched (Fig. 12b). This feature is otherwise unknown in arrows from Eastern family areas, but is seen on arrows from Lagaip River (West Central family) and Duna. Three arrows from Laiagam (West Central family) using variant (i) lightly incised (Fig. 13c) were likewise far removed from the norm of their area, but resembled arrows from Eastern and East Central family areas. I suggest that these five arrows may be 'introduced' items.

ELEMENT 2: diamond

This element is rarely used singly in designs; its commonest forms are 'eye' variants (usually in opposite pairs), solid diamonds in series, or several concentric diamonds.

Eastern and East Central family areas. In both these areas the concentric form is used in designs; the whole is smeared with red-brown ochre.

Central family area. More use is made of this element in the western half of this area. In the eastern part, Chimbu arrows show some use of variant (i) in concentric form. On Wahgi valley arrows, but more frequently in the Hagen area, it is mainly used in 'eye' variant forms. Tambul arrows show use of variant (v) elongated and deeply carved, often in the centre of a two-element, one-motif design (Fig. 15b), with white infill. Yamaga, Mt Hagen, arrows use variants extensively. Variant (iv) as an opposite pair, in the centre of a similar upper and lower motif separated by a central motif not using this element; deeply carved with red and white infill. Variant (i) in upper and centre motifs of a tri-motif design with variant (iv) as well in upper and in lower motif; carving medium deep, red and white infill (Fig. 14a). Variant (v) in opposite and alternate pairs as part of lower motif (Fig. 18c).

Western Central family area. Designs show extensive use of this element throughout the area, deeply carved, with red and white infill. In the northern part 'eye' variants are the most used, especially in Lagaip river area:

1. As the centre of the motif in short designs, variant (iii) or (iv) as one opposite pair, or two pairs opposite and alternate (Fig. 14b).
2. As the centre of a short motif at the shaft when the remainder is barbed, variant (iii) (Fig. 14c).
3. Next to shaft, an opposite pair of variant (iv) (Fig. 14d).
4. As part of upper and lower motifs variant (iii), in a two-motif design separated by an undecorated area (Fig. 29d).
5. Opposite and/or alternate pairs of variant (iv) or (v) at ends of design (Fig. 29e).

Porgera arrow designs use variant (iii) or (iv) at the lower ends at the shaft (Fig. 29c). Variant (iv) in two pairs, opposite and alternate near the shaft, as the only decoration is seen at Arafundi River (Fig. 15d).

In the southern part of this area, designs frequently show a combination of two diamond variants to form a pattern, variant (ii) in series plus an 'eye' variant — (iii) in (Fig. 15a). Iore (Mt. Giluwe) designs, using an 'eye' variant — with only one other element to form the complete pattern are common (Fig. 30d).

Wiru family-level isolate. Designs use mostly 'eye'

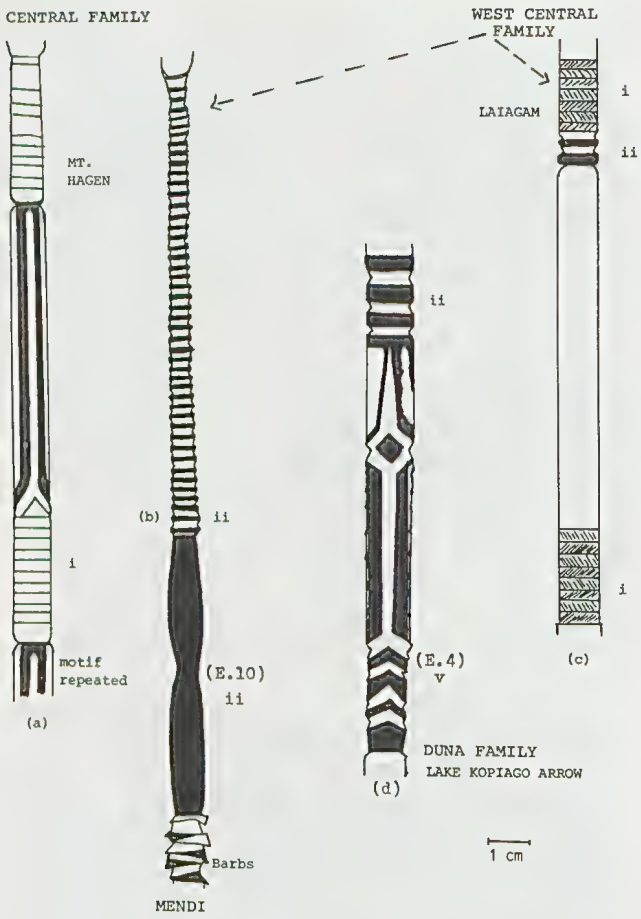


Fig. 13. Element 1 variants in design pattern.

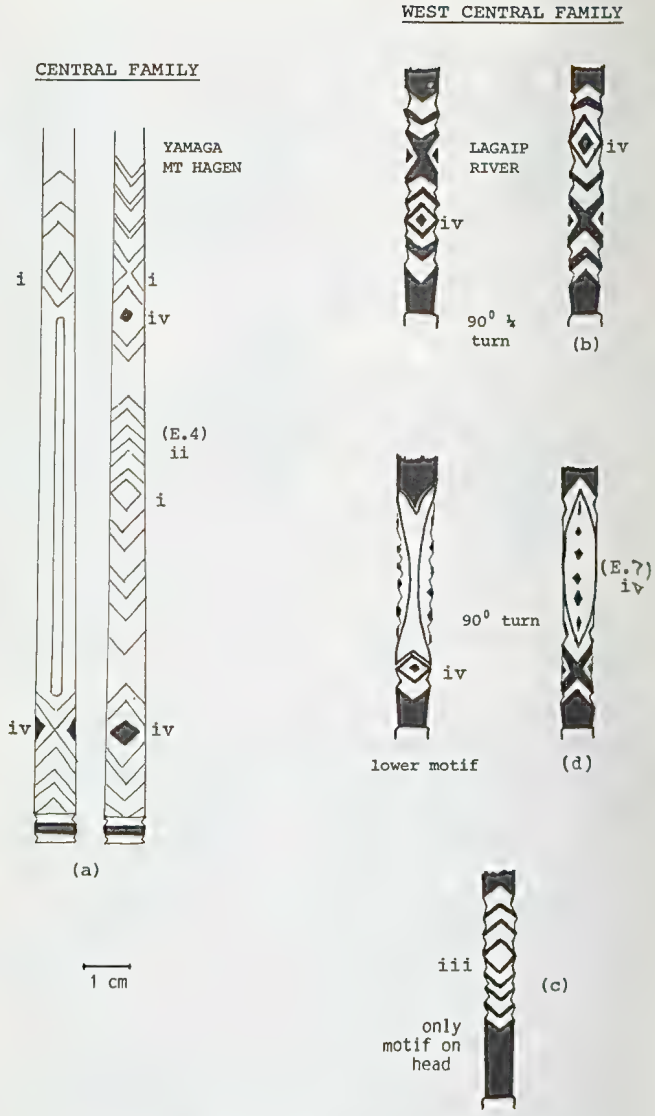


Fig. 14. Element 2 variants in design pattern.

variant (v) with red infill on few arrows.

1. In the centre, three variant (v) around fore-shaft, one (v) with two centres below these (Borona village).

2. As part of upper motif, 12 variant (v), (Borona village).

3. Variant (v) an opposite pair, at upper end of main motif, (Borona village, Fig. 23a).

Duna family area. More use is made of diamonds in series together with frequent use of 'eye' variants, with red and/or white infill.

1. Variants (ii) or (iii) in series as either the upper or lower half of a two-motif design. The lower position seems more favoured on Lake Kopiago arrows (Fig. 16e).

2. 'Eye' variants in the centre of a design to separate two different motifs that occupy all the fore-shaft. The type of variant used seems to relate to the design pattern. Variant (iv) is always the upper element in the lower motif, or the 'centre-piece' of the complete design when upper and lower motifs are the same. When variant (iii) is used, it seems to be in the design solely to separate the upper and lower motifs, with no relationship to either one (Lake Kopiago arrows, Fig. 31).

3. Variant (iii) at lower end of design (Lake Kopiago, Fig. 31b).

4. Variant (iv) as lower motif around head (Lake Kopiago, Fig. 15c).

5. Variant (iv) in centre and (v) at lower end of design covering fore-shaft (opposite pairs) Lake Kopiago, Fig. 31a).

Ok family area. 'Eye' variants infilled with white clay are used most.

1. Variant (iii) or (v) as the topmost element in the design pattern or at the upper end of a short design before barbing starts (Telefomin, Fig. 29a).

2. Variant (iv), an opposite pair, in lower motif near shaft (Tifalmin, Fig. 29b).

3. Variant (ii), surrounded by deeply carved, interlocking and concentric (i), around the head as the only motif before barbing starts (Upper Fly and Telefomin, Fig. 33).

Comments on use of Element 2. Designs on arrows from West Central and Duna family areas indicate a similar use of variant (ii) in series, plus variant (v). Although less use is made of this element in Ok designs,

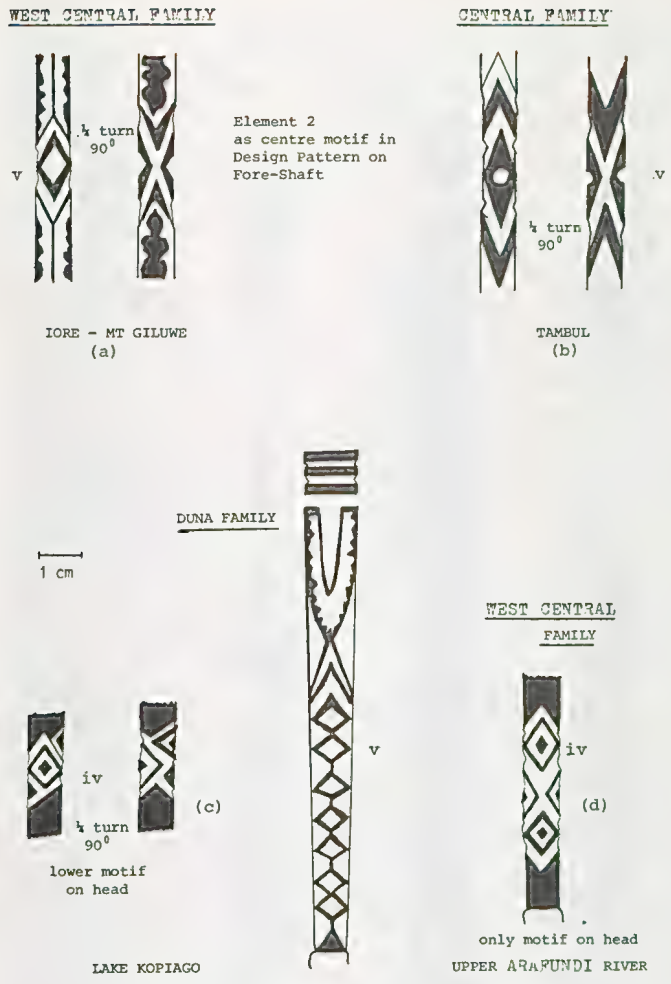


Fig. 15. Element 2 variants in design patterns.

it does occur in some designs on arrows from all parts of the area. In the northern part of West Central, Duna and Ok family areas, 'eye' variants are often used in designs with element 9 variant (iv). This combination will be discussed later.

ELEMENT 3: triangle

Eastern family area. The most commonly used variant is (i) in concentric form (Fig. 12c). East Central designs variants (i) or (v) occur as the main motif (Bena Bena, Fig. 16a). Central area arrow designs use these same two variants similarly positioned, and as well, variant (iii) on heads, at the shaft before barbing starts.

West Central area. More use is made of variants in the southern part, where one or two only are used to form the complete pattern. In Mendi–Iore (Mt Giluwe) region, variants are used extensively; variant (ii) in two alternate rows, linear series (Iore, Fig. 16d); variant (v), inverted cones with medium-deeply carved triangles on each one forming the upper motif in a two-motif design (Mendi, Fig. 16c).

Wiru family-level isolate area. Designs show frequent use of variants sometimes combined to form the complete design (Borona village, Fig. 16b).

Duna family area. Variants are often used as a short motif at the shaft, the only design on the head before barbing starts. Sometimes concentric triangles are used, or variant (iii) deeply carved, alternately inverted and separated by deep grooves. Triangles in series occur as the lower motif in two-motif design patterns which seem to be confined to the Lake Kopiago region (Fig. 16e).

Ok family area. Deeply carved, with red and white infill, variant (i) as the only motif, at the shaft before barbing begins. This variant is also used in two sets on the concave surface of a bamboo head, in concentric form on Upper Fly arrows (Fig. 17b). Variant (iii) alternately inverted as part of a short, geometric pattern on the concave surface of a bamboo head (Telefomin, Fig. 17a). When used thus on the head, this variant is absent from the fore-shaft design.

Comments on use of Element 3. The frequent use of variants in West Central area designs is obvious from Table 8, but designs in the northern part indicate little use is made of this element. Arrows from the southern part and from Wiru area show variety in the use of variants in design patterns. There is also variety in the use of colour infilling designs, especially in Wiru arrows, where yellow and the rare blue pigment, vivianite, are used as well as red and white. In Duna area designs, short motifs are the norm; this is opposite to their length on arrows from the southern part of West Central, where motifs occupy an extensive area of long fore-shafts. In the Ok family area the use of this element in designs seem to indicate individuals 'play around' with ideas on how to use a variant in a different way to the accepted norm, and come up with surprising results. As well as these designs appearing to show individualism in the use of variants, bamboo heads are decorated here more than in any other area, with triangle variants used often in such decoration (Fig. 17a,b).

ELEMENT 4: chevrons and zigzags

Variants of this element are used in arrow designs throughout the highlands and further west. Variants (i), (ii) and (iii) — chevrons — never occur singly. They are used in sets or in opposition, frequently enclosing another element, often to form the complete design. Zigzags, variants (iv) and (v), occur rarely in singular form as boundary marker(s) but usually are used in designs in the same way as chevrons.

East and East Central family arrows show a similar use of variants as part of a design.

Eastern family area. Chevrons, lightly incised, most favoured.

1. Variant (ii) as two sets of chevrons, one in both upper and lower part of a single motif design (Heganofi, Fig. 18a).
2. Variant (iv) zigzags in a group, form the largest and top part of the upper motif, in a two-motif separated design.
3. Variant (i) as upper part of upper motif (Yabwiara, Fig. 12c).
4. Variant (v) as upper part of the design on a short, thick fore-shaft with one (v) at lower end (Upper Ramu, Fig. 18b).

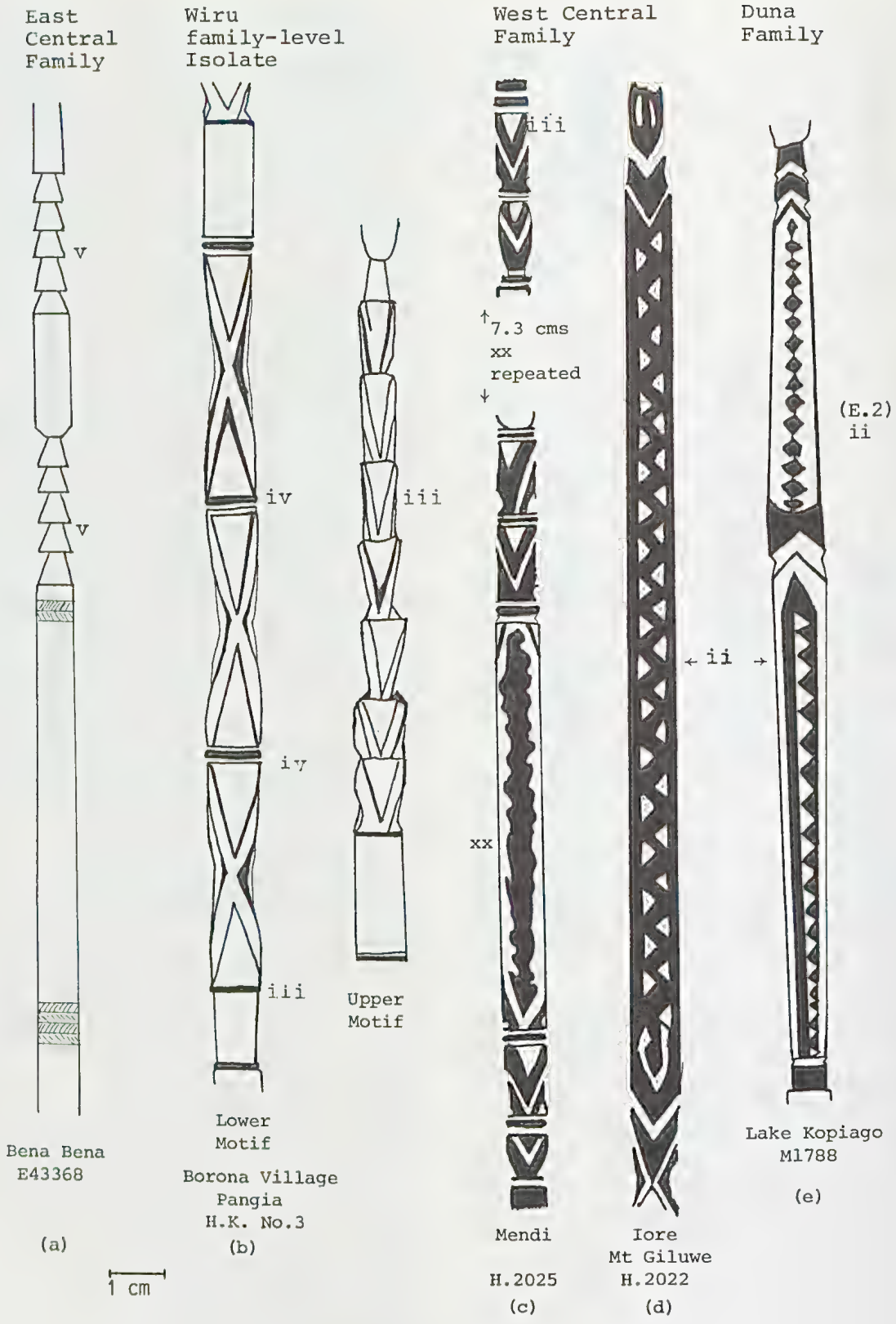
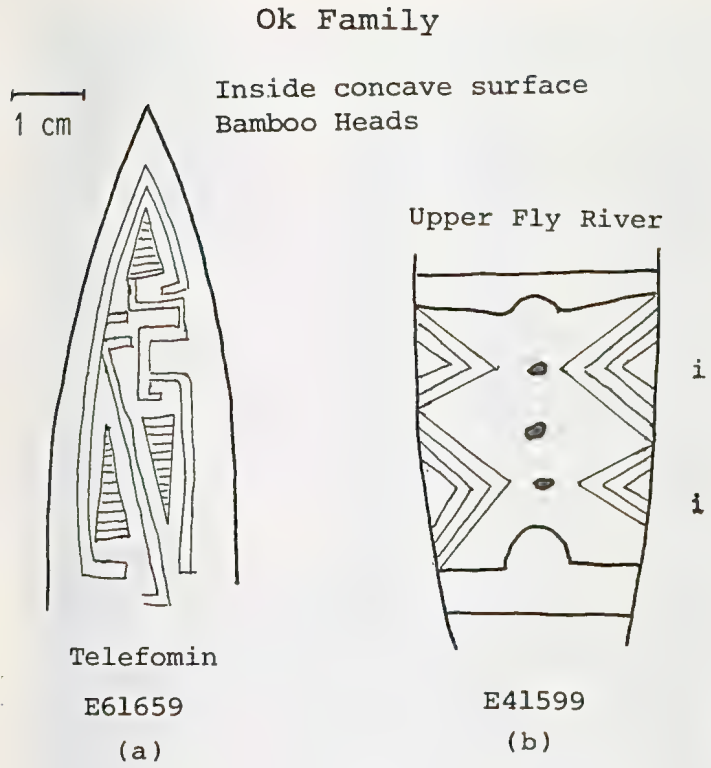


Fig. 16. Element 3 variants in design patterns.



East Central family area. Zigzag variants most used. Variants (iv) or (v) as rows of vertically positioned zigzags on the wider-shaped lower end of the head, as the only decoration on barbed arrows; on Bena Bena arrows carving is medium deep with red ochre infill (Fig. 32a).

Central family area. The Chimbu region and Mt Hagen–Tambul area make most use of variants. Variation in depth of carving designs is very evident, ranging from light (Mai village, Chimbu) to medium (Mt Hagen, Fig. 18c), to very deep in Tambul arrows (Fig. 18e)). Where carving is deep, red and/or white infill is used.

1. Variants (i) and (ii) lightly incised, at both ends of design (Mai village, Chimbu).
2. Variant (iii) medium-deeply carved, forms the main central design motif on one side of the fore-shaft (Yamaga, Mt Hagen, Fig. 14a).
3. Variant (v) very deeply carved, enclosing two sets of opposite pairs of elements 2, variant (v), occupies the complete fore-shaft (Tambul, Fig. 18e).
4. Variant (iii) light to medium deeply carved, occupies the long central area of the design, with variant (i) at the lower end and variant (v) at the upper end (Yamaga, Mt Hagen, Fig. 18c).

Fig. 17. Element 3 variants in design patterns.

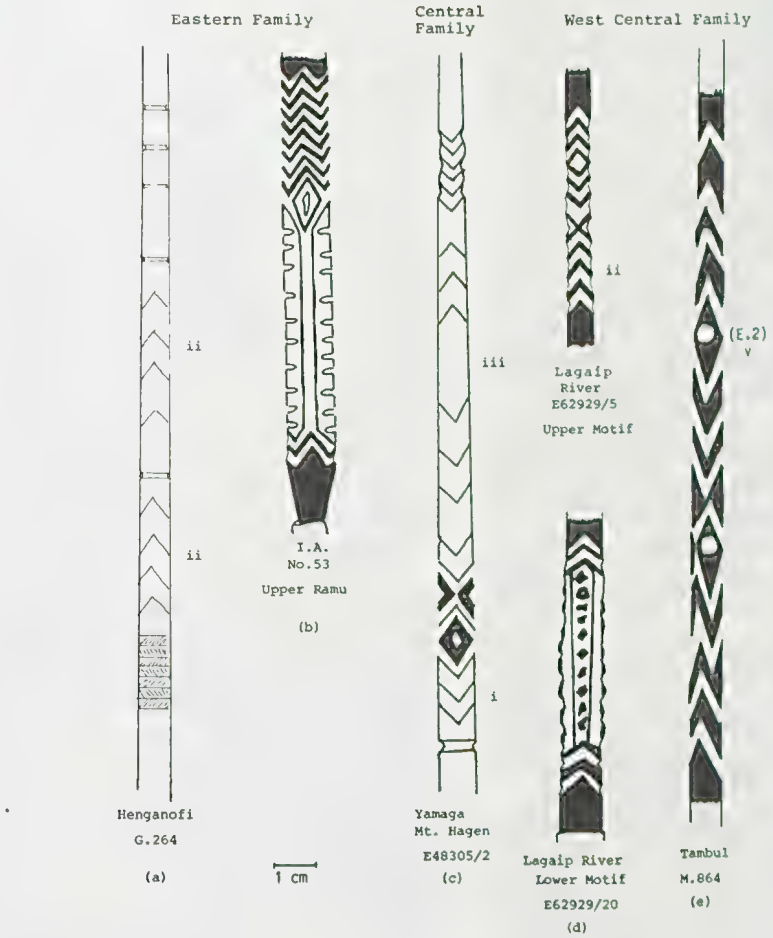


Fig. 18. Element 4 variants in design patterns.

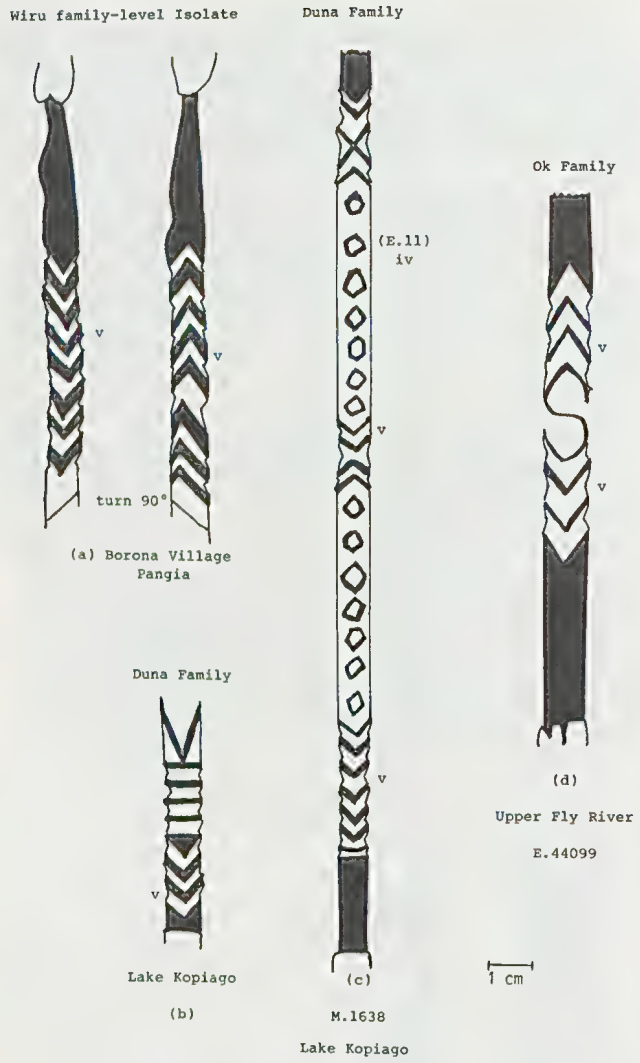


Fig. 19. Element 4 variant (v) in design patterns.

West Central family area. This element is used more in the northern part especially in the Lagaip–Porgera area.

(a) Northern region. 1. Variant (v) deeply carved zigzags, in short lengths of design, separate the other element in a two-element motif that forms the complete design pattern (Lagaip river, Fig. 18d).

2. Variant (v) in a group, near the tip of the head, as the topmost element in a single motif design (Porgera).

3. Variant (iii) as upper motif, deeply carved, enclosing two pairs of 'eye' variants, element 2, opposite and alternate to each other, (Lagaip river, Fig. 18f).

4. Variant (iv) on Keltiga arrows is used around the head, near the shaft, before barbs commence (Fig. 33).

5. Variant (iii) opposing chevrons deeply carved, as the complete design, enclosing 'eye' variant of element 2 (Porgera, Fig. 14c).

6. Variant (v) at shaft (Tabua village, Fig. 20a).

(b) Southern region. Around Ialibu–Mt Giluwe–Mendi, variation in the use of this element's variants provides diversity in designs, and some unusual use of variant (iii) is made. Sets of chevrons occupy the whole design area, enclosing in upper and lower parts a pair of 'eye' variants of element 2. the angles of the chevrons may be connected by a very narrow uncarved area left between them, as at Mt Giluwe (Fig. 30e).

Wiru family-level isolate area. On a few arrows variant (v) is used rather extensively, in designs deeply carved with blue, red and white infill (Borona village, Pangia Fig. 19a).

Duna family area. Designs show the rare use of variant (i), much use of variant (v) deeply carved, infilled with red or white (Fig. 19b,c).

Ok family area. Especially in the Telefomin and Upper Fly areas, deeply carved variant (v) is used to enclose another element (Telefomin, Fig. 29b; Upper Fly, Fig. 19d).

Comments on use of Element 4. A common use for variants (iv) and (v) is as zigzags in unconnected rows, either along the vertical axis of the head or around the head commencing at, or near, the shaft and continuing to where barbs begin. When used this way they are the only added decoration to barbed arrow heads. Either variant is used, apparently at random, except that on arrows from Duna and Ok family areas, variant (v) is used exclusively on barbed heads. Another difference noted is that, whereas on West Central arrows (Gadio people) only one row of zigzags occur vertically along each side of the head, on arrows from other language areas to the east, two or more rows are carved on each side. On Keltiga (West Central) and Mt Hagen (Central) arrows, variant (iv) is used around the head below the barbed area. Another variation occurs on some Baiyer River (West Central) arrows where two rows of zigzags, vertically disposed, cross-over each other forming a pattern below the barbs. On West Central, Duna and Ok barbed arrows, similar short designs seem to favour more the use of variants of elements 2 and 3 (Figs 32, 33).

ELEMENT 5: four-sided figure with short sides inverted, long sides meet in acute angle.

ELEMENT 5A: the same except short sides everted

These elements are absent in designs on arrows from Eastern, East Central and Central family areas and Wiru family-level isolate.

West Central family area. Elements absent on arrows from the southern part of this area, except for one documented from Tabua village where variant (vii) is the only one used in the design pattern along 29.5 cms of fore-shaft (Fig. 20a). In the northern part, frequent use is made of variants of these elements which often have a line of solid dots or rectangles in the hollowed-out centre. Where this occurs I shall write '(dots)' after the variant.

Element 5. 1. Variant (v) in its centre encloses another element to form a short, one-motif design near the shaft (Lagaip river, Fig. 20b).

2. Variant (iv) '(dots)' as upper element in the lower motif of a two-motif design (Porgera).

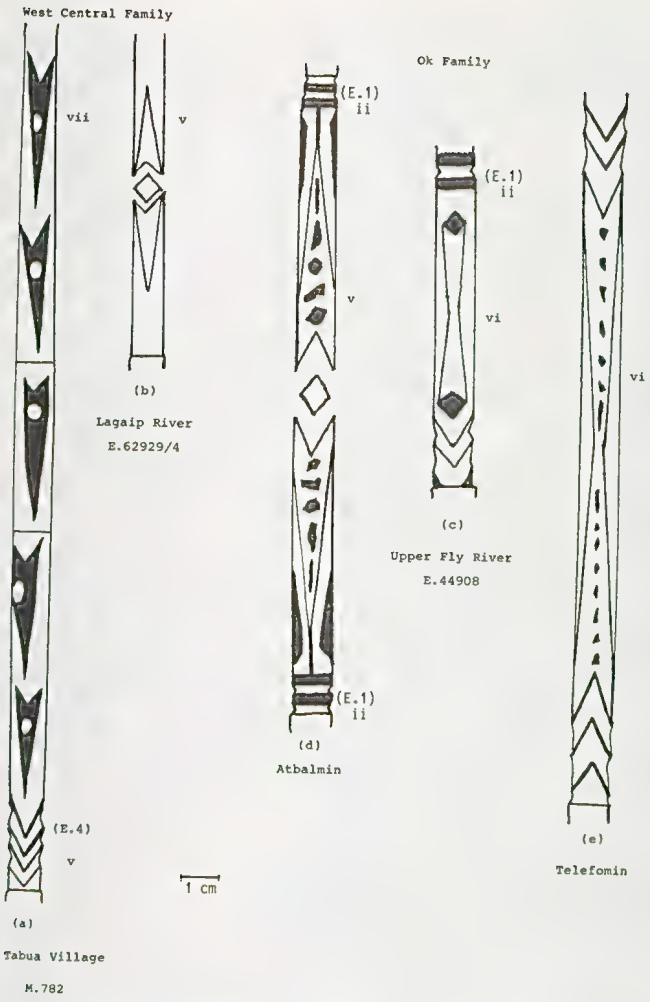


Fig. 20. Element 5 variants in design patterns.

Element 5A. 1. Variant (i) '(dots)', in centre of a one-motif design near shaft (Lagaip river).

2. Variant (ii) '(dots)' as part of upper motif, with variant (iv) '(dots)' as part of lower motif in the same design pattern.

3. Variants (i) and (ii) '(dots)' form upper part of lower motif.

4. Variant (ii) '(dots)' in upper part of geometric design (Porgera, Fig. 27a).

Duna family area. Variants of element 5 only are used.

1. Variant (iii) as part of both upper and lower repeated motif in a separated two-motif design.

2. Variant (v) as part of upper and lower motif. Here it encloses another element and forms the same design on both sides of the arrow head.

Ok family area. Both 5 and 5A are used in designs.

1. Variant (vi) occupies almost all the area in a short design at the shaft (Upper Fly River, Fig. 20c).

2. Variants (iii) and (iv), as opposite and alternate pairs, occupy the complete head (Upper May River).

3. Variant (v) '(dots)' enclosing another element occupies all the fore-shaft on one side, with variant (vi) '(dots)' occupying the reverse side (Atbalmin, Fig. 20d).

4. Variant (ii) '(dots)' as the lower and centre motif in a tri-motif design, with variant (iv) occupying the same position on the reverse side of the fore-shaft (Tifalmin).

5. Variant (vi) '(dots)' occupies all the fore-shaft with element 4 variant (v) as boundary markers (Telefomin, Fig. 20e).

Comments on use of Elements 5 and 5A. The variants of elements 5 and 5A have a limited use in designs on highlands arrows, and a combination of two variants to form part of, or the complete design pattern, is common. Sometimes different variants are used on opposite sides of the same arrow head or fore-shaft to form two different patterns.

In all areas where they are used in designs, these variants are deeply carved, but differ in the use of colour infill. White only is used in West Central and Duna family areas, but in Ok, while red and white are sometimes used as alternate infills, frequently red only is used.

ELEMENT 6: spiral

Spirals are absent from arrow designs of Ok family and Wiru family-level isolate. They are rare in other family areas except West Central, where they occur more in the southern part; in the northern part variants are mainly used as short spirals next to the shaft, often as the only design pattern.

Eastern and East Central family areas. 1. Variant (ii) occurs as a short spiral 5.0 cm long with incised diagonal lines between spiral turns around the head near the shaft, as the only element in the design (Kambira, Fig. 21a).

2. Variant (ii) starting 11 cm from the shaft, a short spiral, 4.3 cm long, separated by circles from a second spiral, 3.2 cm long, which has incised diagonal lines between spiral turns.

Central family area. Deeply carved variant (ii) is the only decoration on a long fore-shaft, 26.2 cm, infilled with white clay (Yamaga, Mt Hagen, Fig. 21b).

West Central family area.

(a) Southern region. 1. Variant (i) almost just curved lines that do not completely encircle the fore-shaft along its whole length (Iore, Mt Giluwe, Fig. 21d).

2. Variant (ii) spirals enclose one other element alternately between their curves, covering the complete fore-shaft in a one-motif design pattern (Ialibu, Fig. 30b).

3. Variant (ii) deep, wide spirals cover the whole fore-shaft, with two circles, one red, one white, as boundary markers at either end (Iore, Mt Giluwe).

4. Variant (ii) forms the lower half of a two-element design motif covering the whole fore-shaft (Iore, Mt Giluwe, Fig. 21c).

(b) Northern region. 5. Variant (ii), in lower half coloured red, in upper half coloured white, separated from each other by circles in this one-motif design (Porgera).

6. Variant (ii) only design on head near shaft (Lagaip River, Fig. 21f).

	EASTERN ..(39)								EAST CENTRAL ..(60)								CENTRAL ..(276)							
	C	PU	PL	UE	LE	All U	All L	All D	C	PU	PL	UE	LE	All U	All L	All D	C	PU	PL	UE	LE	All U	All L	All
No.arrows El.1 Var.	4 i	8 i	7 i	4 i ii	4 i ii			12 i ii	4 i	5 i	6 i	10 ii	12 ii			15 i	20 i	8 i	9 i	17 ii	15 ii			
No.arrows El.2 Var.			4 i ii										5 ii				28 i	33 i iv	36 i iv					
No.arrows El.3 Var.			6 i ii.		2 i					3 i v	3 i v							3 i v	4 iii v					
No.arrows El.4 Var.	6 iii	18 i ii iv	11 ii		1 v	1 v			19 iii iv v	7 ii	7 ii					23 iv v	41 iii	23 i	25 i	27 i ii v	31 i ii iv v			
No.arrows El.5 Var. El.5A																								
No.arrows El.6 Var.								3 ii								10 ii								
No.arrows El.7 Var.							2 i																	
No.arrows El.8 Var																								
No.arrows El.9 Var.																								
No.arrows El.10 Var.																								
No.arrows El.11 Var. El.11A "																								
No.arrows El.12 Var.																								
No.arrows El.13 Var.								1 iii																

Table 8. Element variants and the number of arrows on which they occurred in each position.

Positions:
C: centre of design;
PU: upper part of motif;
PL: lower part of motif;
U: upper; L: lower;
D: design; E: end.

Duna family area. Variant (iii) short spirals separate occurrences of the other element in a two-element motif at the shaft before barbing starts (Lake Kopiago, Fig. 21e).

Comments on use of Element 6. Variants of this element mostly occur as the complete design in all areas where they are used. The limited positioning of the element could possibly relate to its form, which could discourage its use as part of a motif. An almost exclusive use of variant (ii) is evident in all areas. In Eastern and East Central, notable aspects of the use of variant (ii) are its short length (5.0 cm maximum), light incision and no use of pigments; in other family areas it occupies the complete length (measured maximum 30.5 cm), or most of the head or fore-shaft, is deeply carved and infilled with red and/or white ochres and clays. Many spirals are wide (maximum 4.0 mm) particularly in the southern part of West Central family area. Even in this area, where designs are often infilled with other pigments, only red and white are used to colour spirals.

This element's use appears to have regional significance within West Central language family boundary. In the north it occurs in designs on arrows from the Lagaip–Porgera region, and in the south from Mt Giluwe–Ialibu area where arrow designs show prolific use of spirals.

Arrow designs from comparison area Karimui show a similar use of spiral variant (ii) to designs on Iore and Mendi arrows from the southern part of West Central language family area.

WEST CENTRAL ..(260)								DUNA ..(90)								Ok .. (95)								Wiru ..(14)							
C	PU	PL	UE	LE	All U	All L	All D	C	PU	PL	UE	LE	All U	All L	All D	C	PU	PL	UE	LE	All U	All L	All D	C	PU	PL	UE	LE	All U	All L	All D
13 ii	10 ii	10 ii	19 ii	24 ii	13 i	3 i	2 ii	5 ii	3 ii	3 ii	4 ii	4 ii				6 ii			14 ii	10 ii							3 ii	3 ii			
27 iii iv	15 ii iii	19 ii iii	7 v	20 iii iv v	5 ii v	4 ii v	3 ii	14 iv v	9 ii	16 iii	7 iii		7 ii iii	10 ii iii	3 iv	6 iii	11 iii iv	19 ii iv	5 ii iii						1 v	1 v	1 iii	1 v	1 v			
30 ii v	13 v vii	12 iv v	7 i iii	9 i iii	11 iv v	9 v vii	14 iii iv			13 ii					9 i ii iii	4 v vi	7 v	13 v vi			14 v	2 v	3 i ii		1 vii		2 iii iv	2 iii vii	2 i iii	1 iv	2 iii + iv
27 iii v	10 v	10 v	25 i ii iv v	36 v	7 i v		16 iii iv v	4 v		3 v	25 v	31 v	6 i v		12 v	4 v	3 v	9 iii v	5 v	10 v			5 v		2 v	2 v	1 i		1 v		
17 i	22 iv + ii v	34 i + ii iv v			2 iv		12 i ii vii		11 iii v	13 iii v						1 ii iv v vi	9 i ii iii	12 ii iii iv v			5 vi	9 ii iv vi	6 iii iv vi								
		8 ii			10 ii	10 ii	48 i ii			7 iii																				
	20 ii iv	19 ii iv				18 iii	25 iii + iv ii iv			2 ii								5 iv	4 iv	4 iv			7 iv	1 iv	1 iv	2 ii iii					4 ii ii + iv iii + iv
2 i	5 i	4 i	3 i	3 i	11 i ii	10 i										3 i					3 i	3 i		1 i	1 i	2 i	3 i ii	2 i	1 iv		
35 i ii iv	6 i	29 iii i			3 i			3 i								7 iv	8 i	8 i			11 i iv	4 iv	1 i iv								
19 ii	7 ii	9 i ii																							3 ii	2 ii					
18 i iii	19 i	16 iii iv v	2 iv	2 iv		16 iii iv	17 iii iv			9 iv			7 iv	7 iv	16 iv	7 i	10 i iv	8 i	8 i	6 i			8 i ii	2 iv v	1 iv	2 iv v		1 v		1 iv	2 iii iv
10 ii						9 i										6 ii	13 ii iii	13 ii iii				6 ii	17 iv								
1	13 iii	13 iii				5 iii	9 ii		14 i	14 i iii			15 i ii			7 i	12 ii	12 ii	4 iii												

Table 9. Design elements distribution. ☆ = elements used on two arrows either wrongly documented or trade/gifts from a language family much further westward.

Language Family	Elements												
	1	2	3	4	5/5A	6	7	8	9	10	11/11A	12	13
Eastern	★	★	★	★		★	☆						
East Central	★	★	★	★		★							
Central	★	★	★	★		★							
West Central	★	★	★	★	★	★	★	★	★	★	★	★	★
Wiru	★	★	★	★			★	★		★	★		
Duna	★	★	★	★	★	★	★		★		★		★
Ok	★	★	★	★	★		★	★	★		★	★	★

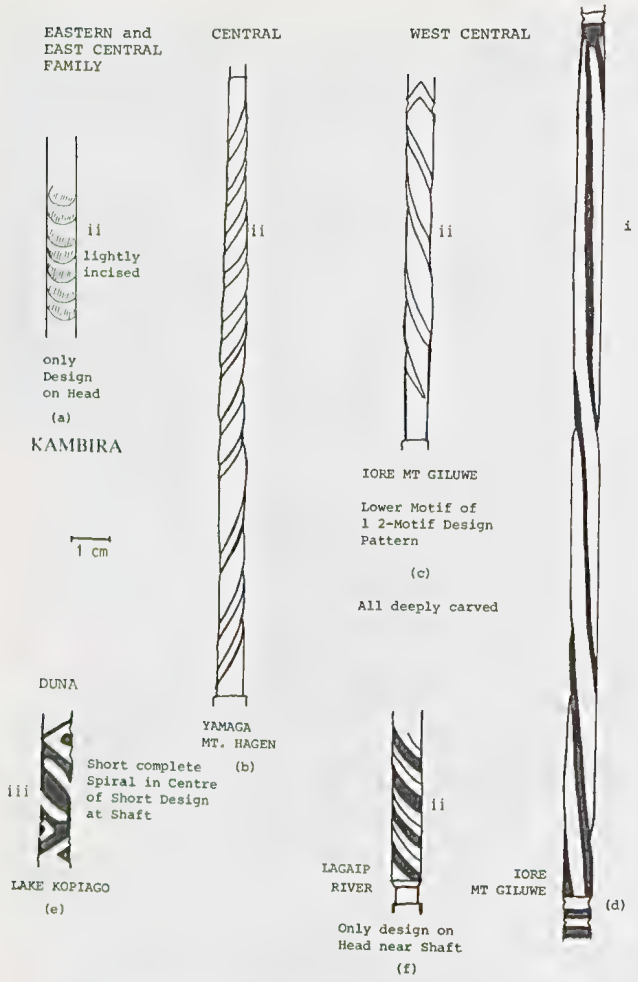


Fig. 21. Element 6 variants in design patterns.

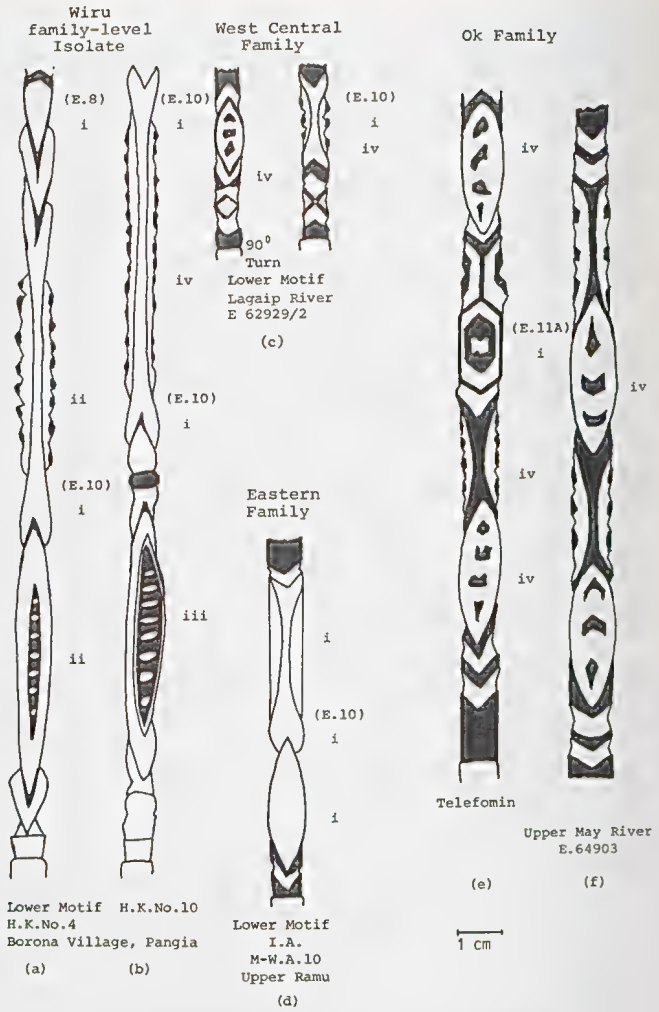


Fig. 22. Element 7 variants in design patterns.

ELEMENT 7: lenticular shield

This element is one of the least used in arrow designs in the highlands except for two family areas, West Central (especially around Ialibu and Mendi in the south) and Wiru family-level isolate. It is rarely present on Duna and Ok arrows, and is absent from East Central and Eastern family areas except for two arrows documented from Upper Ramu.

Eastern family area. As variant (i) medium-deeply carved, two opposite and alternate pairs around fore-shaft as lower motif of a two-motif design (Upper Ramu, Fig. 22d).

West Central family area.

(a) Northern region. 1. Variant (iv) opposite pair, positioned as upper half of a two-element lower motif next to shaft, separated by undecorated area from upper motif using different elements (Lagaip River, Fig. 22c).

2. Variant (iv) as in 1. but here occupying the greater part of both upper and lower motifs, and with one other element ('eye' element 2) forming the whole design pattern (Lagaip River).

(b) Southern region. Ialibu arrow designs frequently show use of variants in elongated form, or combine variants (iii) + (iv).

3. Variant (iv) separated by spiral grooves along complete length of fore-shaft (Ialibu, Fig. 30b).

4. Variant (ii) elongated; two opposite and alternate pairs, enclosed and separated by a different element, form the complete design pattern (Mendi, Fig. 23b).

5. Variants (iii) + (iv) combined to cover the complete fore-shaft. Three of variant (iv) are arranged in a spiral around the lower part. Directly above is an opposite pair of variant (iv) and at the upper end of the design is an opposite pair of variant (iii) alternate to the pair of variant (iv) below (Ialibu, Fig. 30a).

Wiru family-level isolate area. Used most in this area where arrow designs exhibit frequent use of variants elongated and sometimes combined, or individually as opposite pairs to form the whole design.

1. Variant (ii) elongated, two opposite and alternate pairs, occupying most of the lower motif in a two-motif design pattern (Borona village, Fig. 22a). Red, orange and white pigments used to infill design.

2. Variant (iv) elongated, four opposite and alternate pairs, forming a one-motif design, with boundary markers, that occupies the whole fore-shaft (Borona village).

3. Variant (iii), an opposite pair lower motif, plus (iv),

an opposite pair upper motif, with element 10 variant (i), all elongated, covering the whole fore-shaft (Borona village, Fig. 22b).

Duna family area. Variant (iv) occurs as an opposite and alternate pair, as the main element in the lower motif of a two-motif design pattern.

Ok family area. 1. Variant (iv), three elongated, opposite and alternate pairs occupy all the fore-shaft except for another element at both ends of the design (Telefomin, Fig. 26c).

2. Variant (iv), one opposite pair in lower motif of a tri-motif design pattern (Tifalmin).

3. Variant (iv) as three opposite and alternate pairs, two positioned near shaft, one pair at upper end of design, before barbs begin (Telefomin, Fig. 22e).

Comments on use of Elements 7. This element's use in arrow designs documented from Upper Ramu (Eastern family), and its absence from both East Central and Central arrow designs, leads me to suspect these arrows were introduced from an area further to the west.

In the northern part of West Central family area where use of this element is rare, motifs are mostly short and separated by an undecorated area. The variant is reduced in overall size to fit into the long, thin design field provided by the long, slender heads and fore-shafts. In the southern part the opposite happens; variants more frequently occur in elongated form, that is, the curved sides are extended, together with any internal solid areas, to adapt to the long, narrow design area. As well, two different variants are often used in the one design. Some Wiru arrow designs show great similarity, in the use of this element, to those of Ialibu and Mendi, particularly when two variants are combined. However, in Wiru area it is never used with spiral element 6 variant (ii), with which it occurs frequently on arrow designs from the southern part of West Central family area. In Ok arrow designs it occurs in its normal form, as the fore-shafts of these arrows are much shorter and thicker, providing a wider design field for use. In Tifalmin–Telefomin area designs there appear to be an association between the use of variant (iv) of this element and variant (i) of element 11A. This seems to be a regional phenomenon within the Ok family language boundary.

Comparison area Karimui arrow designs show use of variant (i) as the complete lower motif, and as a short, complete design with only variant (i) in two opposite and alternate pairs. All are infilled with greyish clay.

ELEMENT 8: lanceolate, leaf-like shape

Occurs frequently in the southern part of West Central family area, Mendi region, and Wiru family-level isolate area, but in no others except on three arrows from Ok family area. It has two variant forms, both deeply carved; one is carved in linear series along the length of head or fore-shaft, the other is a smaller double-leaf variant in pairs, around the head or fore-shaft.

Wiru family-level isolate. 1. Variant (i) above and below a central element, then variant (ii) as the upper

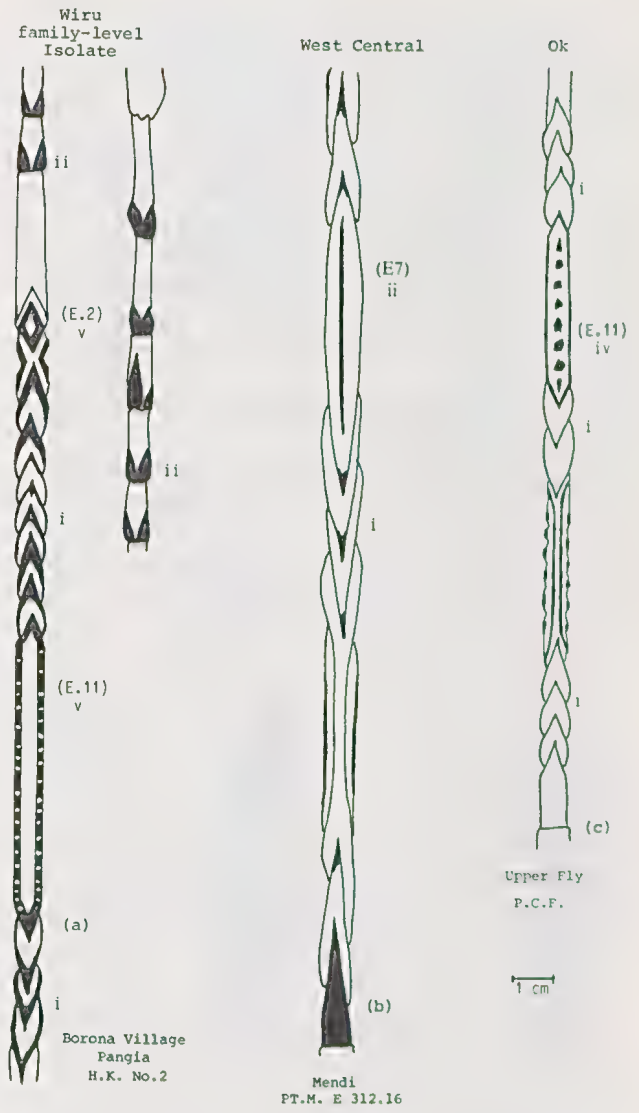


Fig. 23. Element 8 variants in design patterns.

motif in this two-motif design. These are separated by an undecorated area. Red, white and yellow pigments used to infill design (Borona village, Fig. 23a).

2. Variant (i) inverted at upper and lower end of design (Borona village, Fig. 22a).

3. Variant (i) at shaft and in centre, variant (ii) at upper end of a one-motif repeated design (Borona village).

West Central family area. 1. Variant (i) as the main element in a two-element motif covering all the fore-shaft (Iore, Mt Giluwe, Fig. 30d).

2. Variant (i) at both ends and centre of a two-element, one-motif design (Mendi, Fig. 23b).

Ok family area. Variant (i) positioned as upper, centre and lower element, with one other element separating them, in a two-element, one-motif design pattern (Upper Fly River, Fig. 23c).

Comments on use of Element 8. The use of this element is almost confined to the Mendi region in the southern part of West Central family area, and Wiru

family-level isolate area. Variant (ii) is much less used, and then always with variant (i) which lends itself most effectively to use on the long, slender fore-shafts of West Central and Wiru area arrows. Variant (i) is used on Wiru arrows to enclose variants of element 11, whilst Mendi designs use a variant of element 7 in this same way. Upper Fly (Ok family) designs exhibit the use of variant (i) in a similar way to Wiru and Mendi. All are deeply carved with much use of coloured infill. Arrows from Ok family area using this element are almost replicas of those from Wiru, and I suggest these, documented to the Upper Fly, are trade items from Wiru area.

ELEMENT 9: figure with two long sides curved and short sides inverted

In design patterns, variants, especially variant (iv) the 'heart' variant, are frequently associated with 'eye' variants of element 2.

West Central family. 1. Variant (ii), three opposite and alternate pairs, as the centre element in a tri-motif design. Lower motif contains 'eye' variant (v) of element 2 (Porgera, Fig. 24a).

2. Variant (i), two opposite and alternate pairs, in centre as in 1.

3. Variant (iv) centre motif in a tri-motif design. Lower motif contains 'eye' variant (iv) of element 2 (Porgera, Fig. 29c).

4. Variant (iii) in reverse position, an opposite pair, in the lower motif; variant (iv) as central motif, with 'eye' variant (v) of element 2 as the upper motif, in a design covering all the head except for pointed tip. 'Eye' variants (iii) + (iv) of element 2 are associated in lower motif (Lagaip River, Fig. 29e).

5. Variant (iii), two opposite and reversed pairs in lower motif. Opposite and alternate pairs of variant (iv) occupy the remainder of the design area of the head (Lagaip River, Fig. 24b).

Duna family area. 1. Variant (i), very deeply carved, two pairs opposite and alternate at upper end of design (Lake Kopiago).

2. Variant (i) as central motif in a tri-motif design (Lake Kopiago).

Ok family area. 1. Variant (i) as an opposite pair in west motif of a tri-motif design (Telefomin, Fig.

ariant (i) as an opposite pair near shaft with sed pair above, enclosing a variant of element 12. opposite and alternate pair at the upper end complete the design (Tifalmin, Fig. 24d).

3. Variant (i) in two pairs deeply carved, opposite and alternate, forming the upper motif in a two-motif design (Telefomin, Fig. 24e).

4. Variant (iv) in seven pairs, deeply carved, opposite and alternate, in centre position of a tri-motif design, with 'eye' variant of element 2 in upper motif (Telefomin, Fig. 29a).

5. Variant (iv) occupying 24.5 cm of head, eleven down one face of head (unpaired), as the main motif in the design which has an 'eye' motif at the shaft (Tifalmin, Fig. 29b).

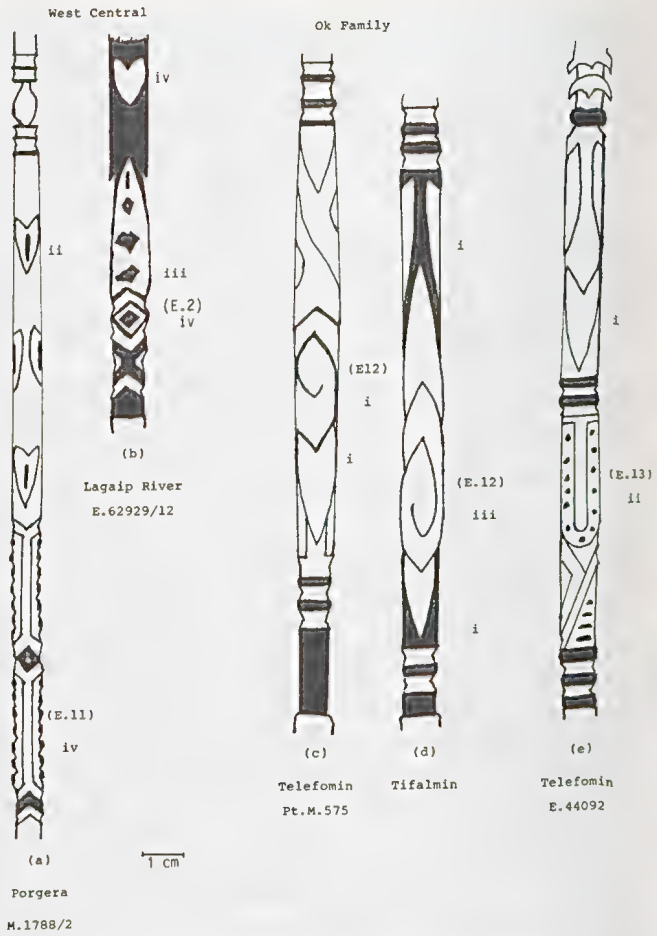


Fig. 24. Element 9 variants in design patterns.

Comments on use of Element 9. This element's distribution appears confined to specific areas within the language family boundaries: Lagaip–Porgera in West Central, Lake Kopiago in Duna, and Tifalmin–Telefomin in Ok. This could point to its diffusion from west to east or east to west (most probably the former), for there is great similarity in its use in Ok and West Central arrow designs. Both show that when variant (iv) is used, either alone or with variant (iii), it is always associated with one of the 'eye' variants of element 2. Here there could be some biological inference in this association, as variant (iv) is heart-shaped, giving a 'hearts' and 'eyes' combination (Fig. 29).

Some bamboo heads on Ok family arrows exhibit the use of variant (i), either carved as on fore-shafts or completely carved-out leaving a hollowed-out outline. When this variant is used on bamboo heads, a different element is used in designs on the fore-shafts. For this element, white infill is usually used, and red is rare.

An unusual method of using variant (iv) is seen on some Tifalmin and Telefomin arrows, which deviate from the norm in two respects. Here the element is not used in pairs, nor is it carved around the head. Instead it is presented in linear series and on one face only of the head, for about 20.0 cm of its length. Positioned directly above an 'eye' enclosed in chevrons at the shaft, is the smallest of a series of variant (iv), 'heart'; above

this they gradually increase in size to two large central 'hearts', then decrease in size towards the tip of the head. In series these numbers are 4–2–4 (Fig. 29b). On other arrows the series are 4–1 (large)–3(small) repeated up to the tip. I think these arrow designs are the work of one artist-decorator, perhaps trying out a different way to use a familiar element in an arrow design.

ELEMENT 10: hourglass

This element has a limited distribution, occurring in West Central family area, Wiru family-level isolate, comparison areas Karimui and Aiome, and on one arrow from Eastern family area.

West Central family area and Wiru family-level isolate. 1. Variant (i) elongated, enclosing in the V-shaped ends another element, in a repeated design motif (Borona village, Fig. 22b).

2. Variant (i) alternate and opposite as part of a motif that covers the whole fore-shaft, repeated four times (Mendi and Borona village, Fig. 22a).

3. Variant (i) as part of lower motif in a separated two-motif design pattern (Lagaip River, Fig. 22c).

4. Variant (ii) in the centre, separating two other motifs (Mendi, Figs 25b, 13b).

Comments on use of Element 10. Even in the language family areas in which it is used in arrow designs, this element is used sparingly. Perhaps the simplicity in shape and few variations that can be given to its form, puts limits on its use in designs and makes it a disfavoured element. The use of variant (i) in West Central family area and more frequently in Wiru family-level isolate area, could be related to the use of Element 7 as the other element in these design patterns, because the two shapes conveniently fit together to form a motif. The arrow documented from Upper Ramu, I strongly suspect of being a gift or trade item from Wiru or West Cenral family area.

In comparison areas Karimui and Aiome (Fig. 25c, d), element 10 is used in the central position where part of the head or fore-shaft is carved to this shape, as in Mendi arrow designs.

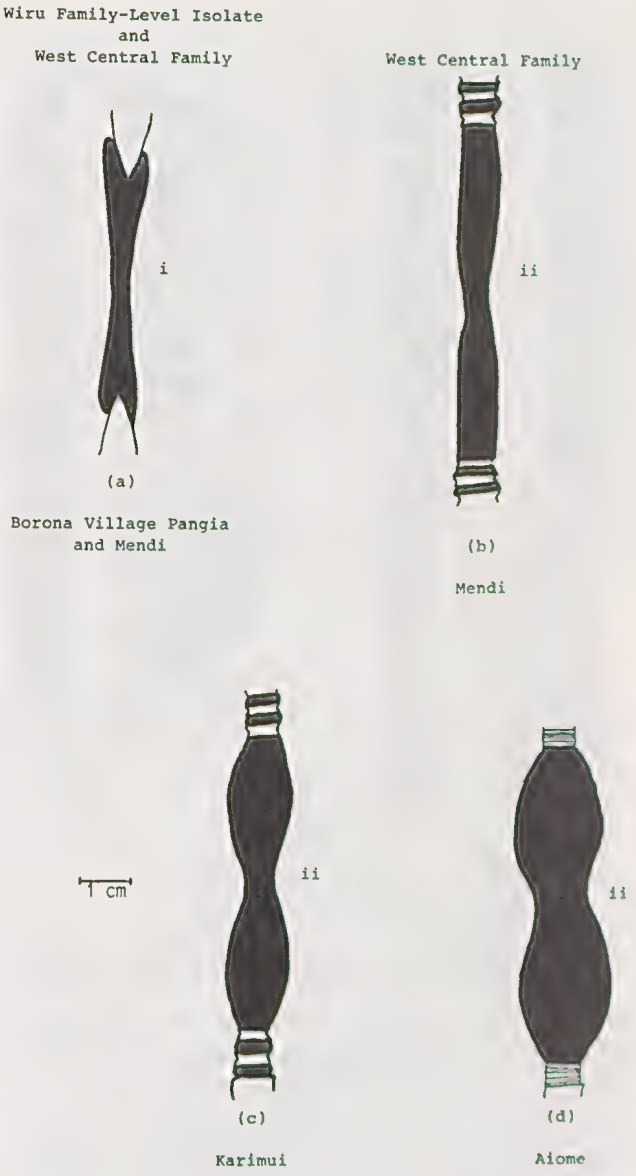


Fig. 25. Element 10 variants in design patterns.

ELEMENT 11: rectilinear, six-sided figure, four short sides everted

ELEMENT 11A: a similar figure with four short sides inverted

Both elements are absent in Eastern, East Central and Central language family areas. Element 11A is found in the Ok family area only.

Element 11 West Central family area.

(a) Northern region. 1. Variant (iv) as complete lower motif near shaft, in a two-motif design separated by an undecorated area (Lagaip River).

2. Variant (iv) as two opposite pairs separated by an element 2 'eye' variant, form the lowest motif in a tri-motif design (Porgera, Fig. 24a).

(b) Southern region. 1. Variant (iii) two opposite pairs in centre of design (Mt Giluwe).

2. Variant (iv) elongated, as two opposite pairs occupying the whole fore-shaft, separated from each other by circles or 'eyes' at the centre of design, boundary marker circles at both ends. Variant (iii) is also used in this same manner.

3. Variant (iii) as an opposite pair; variant (iv) as a opposite and alternate pair above, forming the lo two-thirds of a tri-motif design on a long, slender fo shaft. Both variants are elongated (Mendi, Fig. 3(

4. Variant (iv) as two opposite pairs at upper end a lower motif at shaft, and reversed on repeated upp motif, separated by a different motif at centre (Mendi).

5. Variant (iv) elongated, as two opposite pairs separated by an undecorated area, with a very short variant (iv) completing the fore-shaft design (Tabua).

Wiru family-level isolate area. 1. Variant (iv) elongated, two opposite pairs occupying the whole fore-shaft, separated from each other by circles or 'eyes' at the centre of design; boundary marker circles at both ends. Variant (iii) is also used in this same manner (Borona village).

2. Variant (iv) elongated, as two opposite and

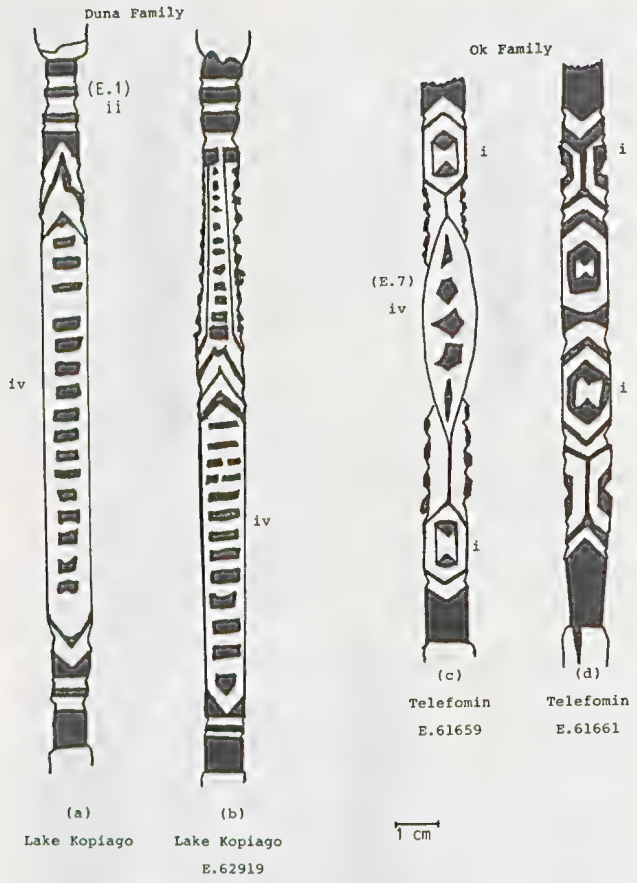


Fig. 26. Element 11 and 11A variants in design patterns.

alternate pairs occupying the lower two-thirds of the design, with a different element in the upper one-third completing the pattern (Borona village).

3. Variant (v) as one opposite pair at lower end of design near shaft, and in centre position in the same pattern; yellow infill (Borona village).

4. Variant (v) as one opposite pair forming the centre element in the lower design, in a separated two-motif pattern; yellow infill (Borona village, Fig. 23a).

Duna family area. 1. Variant (iv) as two opposite pairs occupying the whole fore-shaft, except for zigzags or 'eyes' separating them at the centre, and zigzags enclosing them at both ends (Lake Kopiago, Fig. 19c).

2. Variant (iv) as two opposite and alternate pairs forming the complete design, separated in the centre by zigzags with circles as boundary markers at both ends. Very deeply carved; white infill (Lake Kopiago, Fig. 26b).

3. Variant (iv) elongated to form the complete one-element, one-motif design with circle boundary markers at both ends (Lake Kopiago, Fig. 26a).

4. Variant (iv) as an opposite pair forming the lower motif (Lake Kopiago, Fig. 31a).

Ok family area. 1. Variant (iv), upper element in a two-element motif next to shaft. Different elements complete the design. Deeply carved; coloured red and white (Telefomin).

2. Variant (iv) as two opposite and alternate pairs, together with one other element forming the complete design pattern (Upper Fly, Fig. 23c).

Element 11A. Ok family area. 1. Variant (i) at both ends of a design pattern, in opposite pairs (Telefomin, Fig. 26c).

2. Variant (i) in upper motif of a complicated geometric design (Telefomin, Fig. 27b).

3. Variant (i), four opposite and alternate pairs each separated by a zigzag make the complete design pattern (Tifalmin, Fig. 26d).

Comments on use of Elements 11 and 11A. Although variants of elements 11 and 11A are used in arrow designs in only three of the language family areas and Wiru family-level isolate, variants of 11 are widely distributed throughout Wiru and West Central, as are variants of 11A in Ok area. In Duna arrow design, variant (iv) of element 11 is used exclusively and appears confined to the Lake Kopiago region. In Wiru and West Central area, variants are sometimes elongated to fit the design field on a long, slender head or fore-shaft, and this also occurs in Duna family language area because often only one or two variants are used to occupy the complete design field. Variants are deeply carved in all areas, but coloured clays and ochres used as infills to emphasize them, differ in different areas; in the northern part of West Central area white is used for all variants, but in the southern part, red and/or white is used. In Wiru area, variant (iv) is always infilled with yellow clay, whilst in other variants either red or white is used. In Duna designs, white infill is used exclusively; in Ok arrow designs red and/or white are used.

ELEMENT 12: geometric

Deeply carved, often continues around head or fore-shaft, but frequently used as part of a vertically-placed motif. It was impossible to analyse all geometric variants, so the ones below are selected because they are the four most commonly used in design patterns. They are found in only two family areas: the northern region of West Central, where they are rare, and the Telefomin–Tifalmin region of Ok family area, where they are used extensively.

West Central family area. 1. Variant (ii) as centre element in the central motif of a tri-motif design covering all the fore-shaft (Porgera, Fig. 27a).

2. Variant (i) as the lower motif separated by an undecorated area from the upper motif, in a two-motif design pattern (Lagaip River, Fig. 27d).

Ok family area. 1. Variant (i) in centre position in lower motif, and as mirror image in upper motif on reverse side of fore-shaft, in a two-motif design (Telefomin, Fig. 24c).

2. Variant (ii) as an opposite pair in lower part of design enclosed by a variant of element 9 (Tifalmin, Fig. 24d).

3. Two of variant (ii), one a mirror image of the other, joined as centre motif, and variant (ii) as lower motif next to shaft, in a tri-motif, and variant (ii) as lower motif next to shaft, in a tri-motif design on fore-shaft

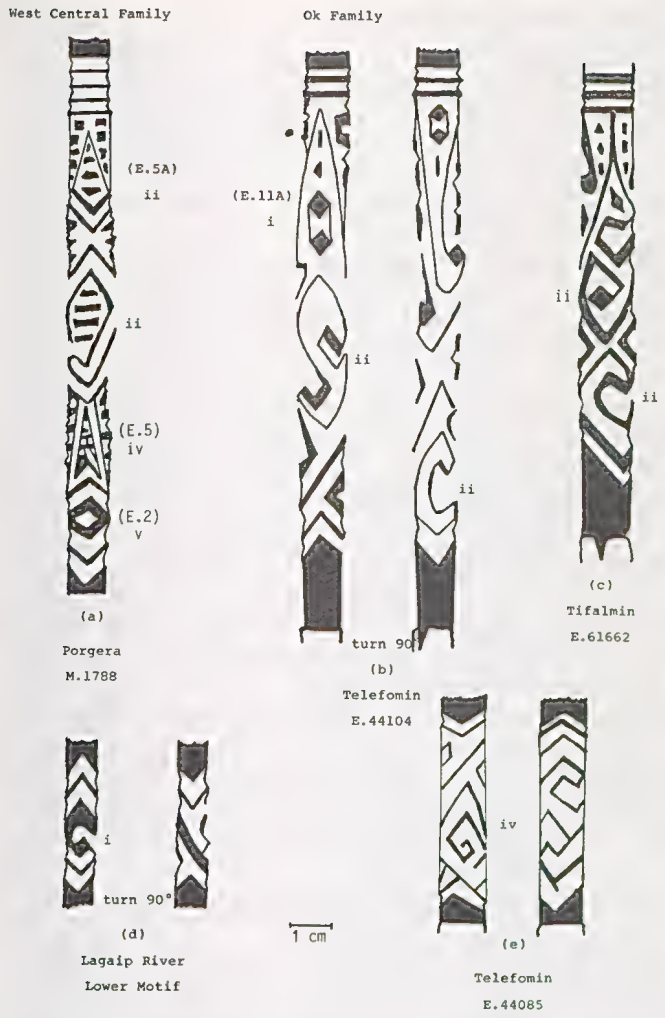


Fig. 27. Element 12 geometric variants in design patterns.

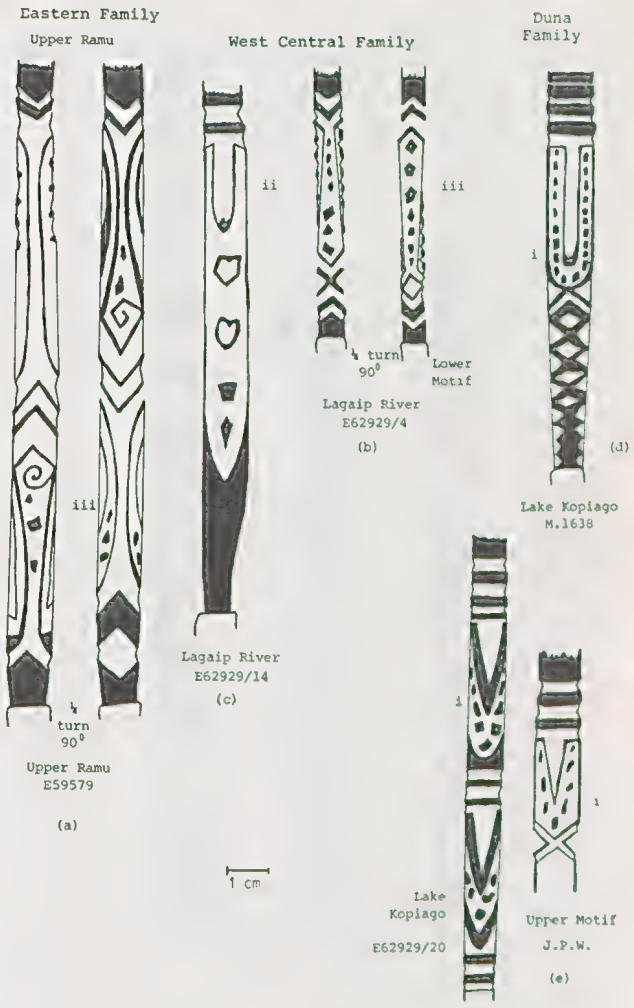


Fig. 28. Element 13 variants in design patterns.

(Telefomin, Fig. 27b).

4. Variant (iv) in a complex angular design, for 5.0 cm on head next to shaft; there is no other decoration (Telefomin, Fig. 27e).

5. Variants (ii) + (iv) in a complex angular design occupying all the fore-shaft (Tifalmin, Fig. 27c).

Comments on use of Element 12. Variants of this element are rarely seen on highlands arrow designs. When used they often occur either reversed or as mirror images in two areas of the design. Variant (iv) is the only one used as the complete design. Sometimes red ochre and/or white clay are used to infill designs, but often no colour is used.

The frequent use of this element in an area of Ok family to the west of Strickland Gorge, and its rare use in the northern part of West Central family area, might indicate its diffusion from west to east, i.e. from Telefomin–Tifalmin area to the Lagaip River–Porgera region.

ELEMENT 13: grooved elements

Very rare in Eastern family area, absent in East Central, Wiru and Central; present in all other areas. Grooves sometimes contain a line of solidly carved dots inside or outside in their surrounding area. Where these occur I shall indicate these occurrences by writing '(dots inside)' for the former, and '(dots outside)' for the latter, after naming the variant concerned.

Eastern family area. 1. Variant (iii) '(dots inside)' occurs twice, one upright at base of lower of two motifs the other time inverted at the top of the upper moti which is itself an inverted example of the lower moti (Upper Ramu, Fig. 28a).

West Central family area 1. Variant (ii) '(dots outside)' surrounds elongated to fill length of whole fore-shaft on both sides, (Lagaip River, Fig. 28c)

2. Variant (iii) '(dots inside and outside)' occupies the greater part of upper motif, and in reversed position in lower motif on opposite side of fore-shaft (Lagaip River).

3. Variant (iii) '(dots inside)' two opposite and alternate pairs, plus 'eye' variant of element 2, form the whole lower motif in a separated two-motif design (Lagaip River, Fig. 28b).

Duna family area. 1. Variant (i) '(dots outside)' as part of upper and lower motifs in a two-motif design (Lake Kopiago, fig. 28e).

2. Variant (i) as in 1. above but inverted in upper motif.

Table 10. Positioning of elements in design patterns.

Language Families
E = Eastern
C = Central
W = Wiru
Ok = Ok
D = Duna
WC = West Central
EC = East Central

Positions
C = Centre of design
PU = Part of upper motif
PL = Part of lower motif
U = Upper
L = Lower
D = Design

Element		C	PU	PL	UE	LE	All U	All L	All D
1	E	*	*	*	*	*			*
	EC	*	*	*	*	*			*
	C	*	*	*	*	*			
	WC	*	*	*	*	*	*	*	*
	D	*	*	*	*	*			
	Ok	*			*	*			
	W				*	*			
2	E			*					
	EC					*			
	C	*	*	*					
	WC	*	*	*	*	*	*	*	*
	D	*	*	*	*		*	*	*
	Ok	*	*	*	*				
	W	*	*		*	*			
3	E			*		*			
	EC		*	*					
	C		*	*					
	WC	*	*	*	*	*	*	*	*
	D			*				*	
	Ok	*	*	*			*		*
	W		*		*	*	*	*	
4	E	*	*	*					
	EC	*	*	*					*
	C	*	*	*	*	*			*
	WC	*	*	*	*	*	*		*
	D	*		*	*	*	*		*
	Ok	*	*	*	*	*			*
	W		*	*	*	*	*		
5A 5	E								
	EC								
	C								
	WC	*	*	*					*
	D		*	*					
5A 5	Ok	*	*	*			*	*	*
	W								
6	E								*
	EC								*
	C								*
	WC			*			*	*	*
	D			*					
	Ok								
	W								
7	E							*	
	EC								
	C								
	WC		*	*			*	*	*
	D			*					
	Ok			*	*	*			*
	W	*	*	*		*			

Element		C	PU	PL	UE	LE	All U	All L	All D
8	E								
	EC								
	C								
	WC	*	*	*	*	*	*	*	
	D								
	Ok	*					*	*	
	W		*	*	*	*	*		
9	E								
	EC								
	C								
	WC	*	*	*			*		
	D	*		*	*				
	Ok	*	*	*		*	*	*	*
	W								
10	E								
	EC								
	C								
	WC	*	*	*					
	D								
	Ok								
	W		*	*					
11 11A 11	E								
	EC								
	C								
	WC	*	*	*	*	*		*	*
	D			*			*	*	*
	Ok	*	*	*	*	*			*
	W	*	*	*		*		*	*
12	E								
	EC								
	C								
	WC	*						*	
	D								
	Ok	*	*	*				*	*
	W								
13	E								*
	EC								
	C								
	WC		*	*				*	*
	D		*	*			*		
	Ok	*	*	*	*				
	W								

3. Variant (i) '(dots outside)' as an opposite pair in upper motif of a two-motif design (Lake Kopiago, Fig. 31c).

4. Variant (ii) '(dots inside)' one pair, upper motif, plus variant (iii) '(dots inside)' inverted, one only as part of lower motif (Lake Kopiago, Fig. 31a).

5. Variant (iii) '(dots inside)' an opposite pair, forming the upper motif in a two-motif design pattern, (Lake Kopiago, Fig. 31b).

6. Variant (ii) '(dots outside)' in an opposite pair as

the upper half of a one-motif design pattern (Lake Kopiago, Fig. 28d).

Ok family area. 1. Variant (i) '(dots inside)' one inverted, forms an opposing pair with another in centre position of design (Telefomin).

2. Variant (ii) as opposite pairs '(dots outside)' forming part of upper and lower motifs in a two-motif design (Upper Fly).

3. Variant (iii) as an opposite pair at upper end of design (Telefomin).

4. Variant (ii) '(dots inside)' as an opposite pair in upper part of a complex lower motif (Telefomin, Fig. 24e).

Comments on use of Element 13. Apart from a single arrow from the Eastern language family area using variant (iii) as its whole design, variants of element 13 are completely absent from designs on Eastern, East Central and Central family arrows. The anomalous Eastern family arrow is therefore assumed to have been introduced much further westwards.

Only in the northern part of West Central area do designs on arrows exhibit the use of variants of this element, and one can say its distribution covers a geographic region from Lagaip River through Lake Kopiago area westwards to the border with Irian Jaya. This distribution pattern points to a linkage between West Central and Duna family areas in the highlands, and Ok family area across the Strickland Gorge.

DISCUSSION OF ELEMENT USE

In this discussion I am excluding two arrows (E59579 Aust. Mus.) documented Upper Ramu, Eastern family area, and three from Laiagam (PNGM) West Central family, because they show no correspondence at all in element use and design patterning to other arrows within their documented areas. These arrows, I am convinced, have come from other language family areas as trade items or gifts.

Data from Tables 7, 8 and 9 show that seven elements (7–13 inclusive) occur only in designs from western areas, which also use twice as many design elements as eastern areas. The numbers of elements used are:

Eastern	East Cental	Central	West Central	Duna	Ok	Wiru
5	5	5	13	10	11	8

From these data, although there appears to be a boundary or break between Central and West Central areas, when tested against a theoretical distribution generated by means of a random numbers table, it was found not to be significant even at P = .05, using a chi-square test. A further similar test gave the result 'probably significant'. However, the use of the 13 elements considered does seem to confirm the idea that there are basic distinctions between design patterns on arrows from the language family areas to the east and west of the suggested physiographic boundary. Designs on arrows from Eastern, East Central and Central family areas are simple and stylistically homogeneous.

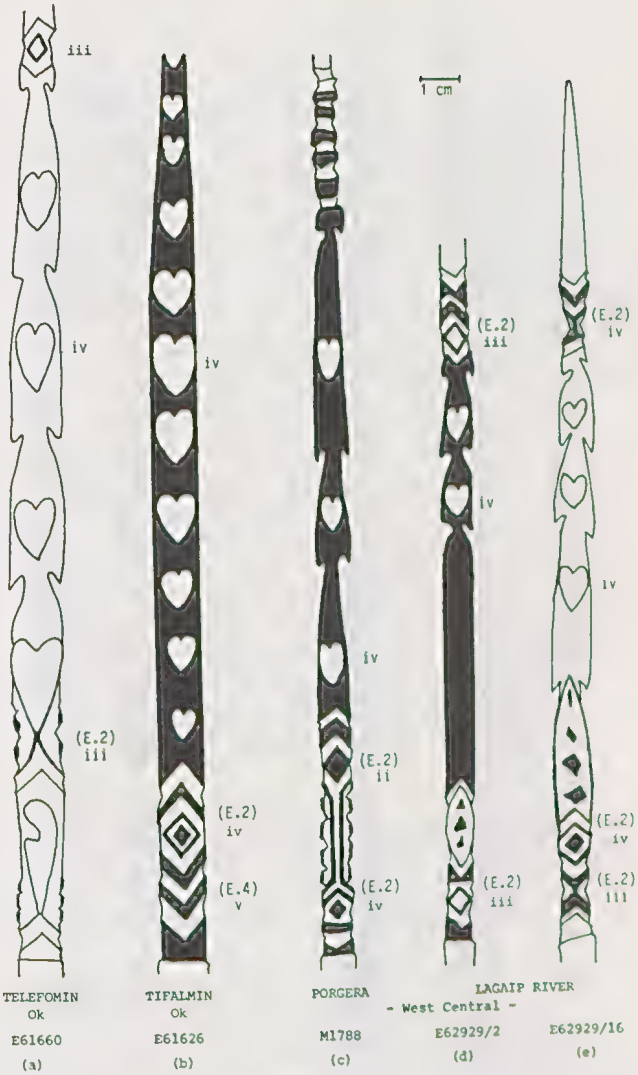


Fig. 29. Design patterns — 'eye-heart' combination. Element 2 variants with element 9 variant (iv).

The small number of elements used limits the similarities possible within their own family groups and also puts constraints on their possible similarity to arrows from those language groups — West Central, Duna and Ok — which exhibit the use of many design elements. The larger the number of elements used in design patterns the greater the variation possible within and between family groups. This is evident in West Central family area where the use of some variants of every element in designs, and the physiographic diversity within an extensive language boundary, results, as could be expected, in the greatest within-group variation. The variation is not in arrow form, but in the elements used in design patterns. Some elements are used only in the northern region, others only in the south; elements 5, 9, 12 and 13 appear confined to Lagaip and Porgera areas in the north, whilst elements 8 and 10 are found only in designs on arrows in the southern region around Mendi, except for the use of element 10 variant (ii) on a few Lagaip arrows. Element 11 is used rarely in the north but frequently in the south; the opposite occurs with the use of elements 3 and 4, which are rare in the

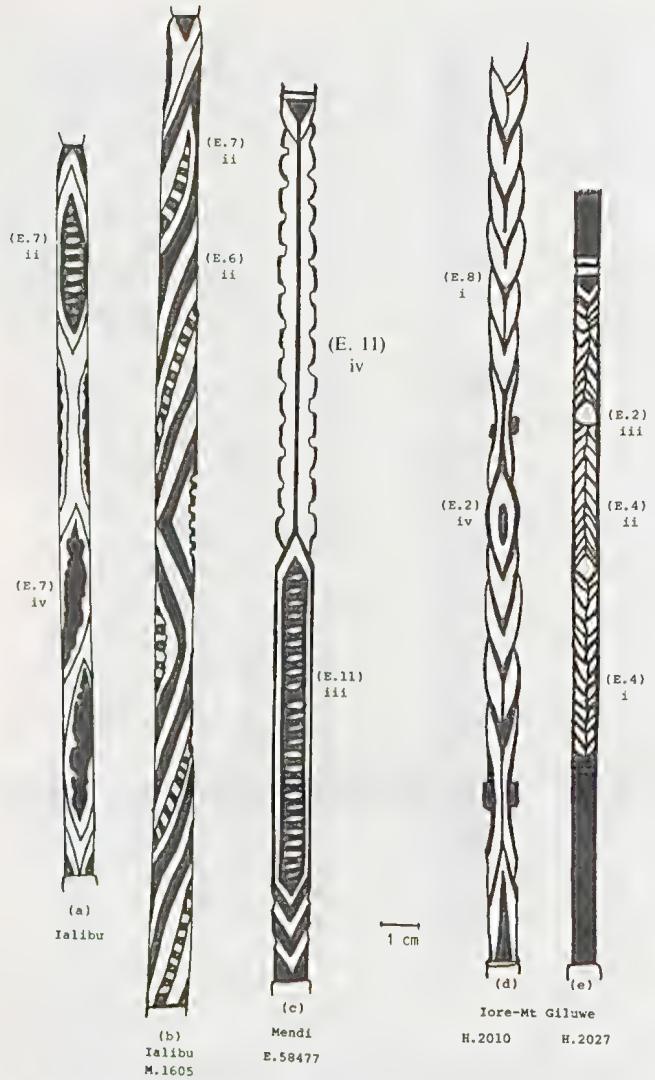


Fig. 30. Design patterns from southern region of West Central.

south. Moreover, in the south, element 3 is never used with element 9 variant (iv), with which it occurs most often in the northern part of this language area. As well, the positioning of motifs to form the design differs: repetition of a motif in unbroken sequence to form a single design pattern on long fore-shafts is confined to the southern region of West Central family area. In the northern region the usual design pattern is a small motif at the shaft separated from an upper motif formed of different elements. Thus there seems to be a division bordering on a dichotomy in element use and patterning within the West Central family area. The boundary of this division in arrow design patterns correlates with the linguistic boundaries of sub-families Enga (in the north) and Angal-Kewa (in the south), within West Central language family area. In the north, element use shows similarities to designs on Duna and Ok arrows, whilst in the south, affinities to Wiru family-level isolate are apparent, as well as to some extent, those of Karimui comparison area.

Ialibu arrow-artists show in their design patterns a distinctive way of using variants of element 7. Their mode of spiralling this element's variants around a fore-shaft to form the complete pattern demonstrates ingenuity and expertise in design giving a uniqueness in style that can only be the work of specialist arrow-decorators. This style is of regional significance within the southern part of West Central family area, for it is not found elsewhere in the highlands (Fig. 30a, b).

Within the Duna family area, the designs seen only on fore-shafts of Lake Kopiago arrows with bamboo heads show a high degree of similarity in elements used, and the positions these occupy within design patterns. These fore-shafts are all comparatively short, with elaborate, deeply carved, two-motif designs, coloured red and white, occupying the complete design field. These traits, and particularly the element-position factor, are so distinctive that they are easily distinguishable from morphologically similar arrows from other areas.

In the use of variants of element 1 (circles), Central family area seems to be a transition zone: Eastern and East Central use only variant (i) in designs, Central uses both variants whilst areas to the west use variant (ii) almost exclusively. In the use of element 2 (diamond), Central area arrow designs show similarities to those of East Central in the eastern half, whilst in the western half, especially in the north, strong affinities with West Central are seen. Element 3 (triangle) in Central is similar to East Central in positioning, using mainly the same variants (i/v), but is medium-deeply carved in Central as against lightly carved in East Central.

In depth of carving there is a very noticeable transition across Central area from light carving in the eastern border area to deep at its border with West Central family area, with medium-deep carving being used for most Central family designs. In general, the border affinities indicated above hold for other elements used in Central family area arrow designs. In the use of colour pigments there is a change from designs without colour or a smearing of red ochre in Eastern family area, through some use of red ochre in East Central, white with some red in Central, to a profuse use of red and white in the northern part of West Central, along with yellow as well in the southern region. Duna and Ok arrow designs exhibit a lavish use of red and white. These correlated patterns in elements used, depth of carving and colours used provide strong evidence to support my contention that Central family area is a transition zone in arrow decoration.

Looking further west, all variants (except (v)) of elements 5 and 5A occur in Ok designs which also show extensive use of elements 4, 9 and 12, while 11A variants are found only in Ok designs. This within-family use of certain elements produces design patterns easily distinguishable from those of other language family areas. There is some indication of a west-to-east diffusion of element 12, from frequent use in Ok designs to rare use in the northern part of West Central, and its absence further east. This, together with restriction

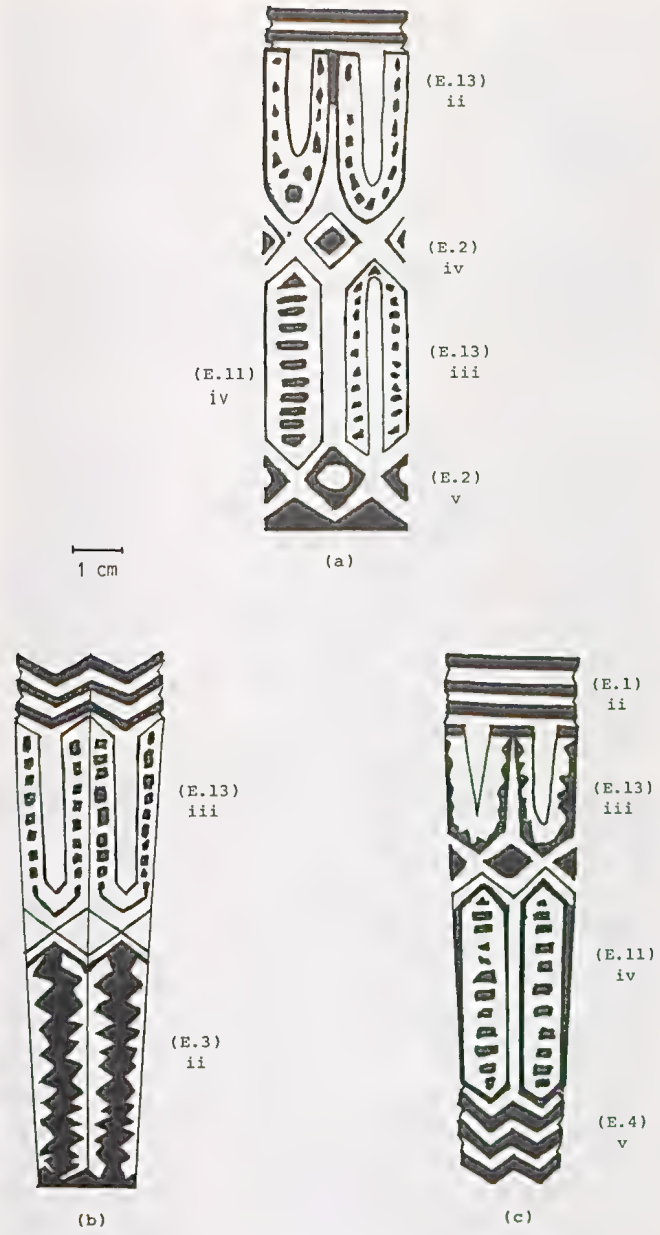


Fig. 31. Lake Kopiago fore-shaft design patterns.

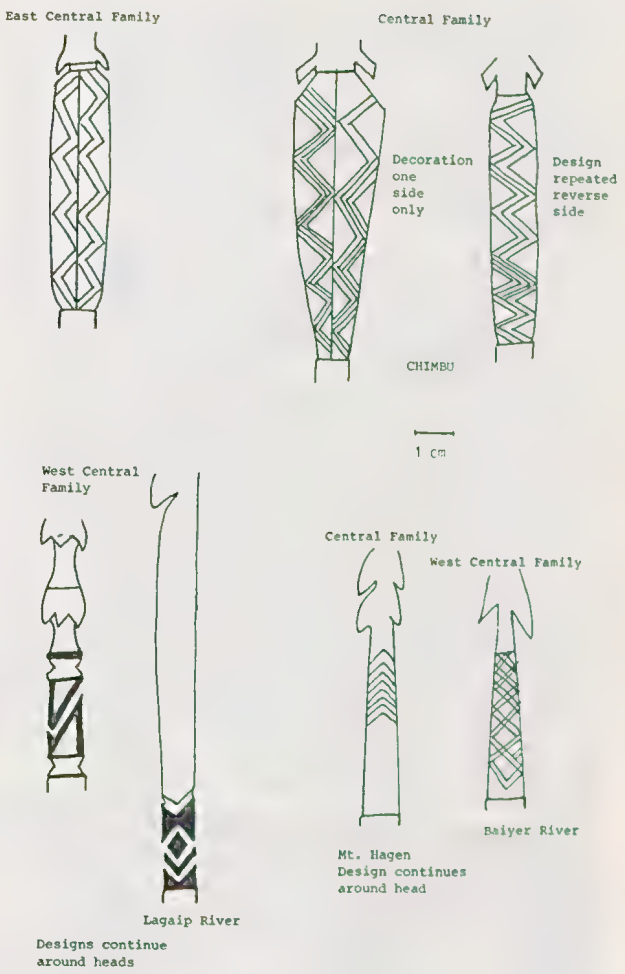


Fig. 32. Designs on heads before barbs commence.

of the combination of 'eye' variants of element 2 with 'heart' variant of element 9 to these two family areas, suggest the Strickland Gorge is not a barrier to design pattern distribution. The fact that variants of elements 5 and 5A, 9 and 13 occur only in designs on arrows from West Central, Duna and Ok family areas, points to the absence of physiographic restrictions on design pattern distribution between these three language family areas.

The Duna people of Lake Kopiago area make much greater use of element 13 variants in arrow designs than occurs in West Central family to the east and Ok family to the west. This use-factor raises questions. Did this element have its origins in the Lake Kopiago area and from there spread to the east and west, or was it an element adopted by the Duna from West Central or Ok and incorporated so successfully in their designs that it became a favoured element of arrow artist-decorators? Early language movements and settlement patterning did not give any positive indication. On the basis of use it would appear that element 13 had its origins in the Lake Kopiago area, even though the distribution patterning of other elements found only in these three family areas seems to point to a movement from west to east.

The similar use of the same variants of some elements in designs on arrows from Eastern, East Central and Central language family areas, indicates the Chimbu–Asaro Divide is not a barrier to design pattern distribution.

Except for the use of element 10 (variant ii) shaped as part of the fore-shaft as it is on some Mendi arrows, I found no correspondence between designs on Aiome (middle Ramu) arrows and those from any language family under study. However, in Karimui comparison area (Daribi speakers), designs on arrow heads and fore-shafts show a close affinity to those on arrows from the southern part of West Central area. Spirals, lenticular shields in various forms, circles and inverted cones seem to dominate design patterns. All are deeply carved, coloured with red ochre and white or grey clay infill.

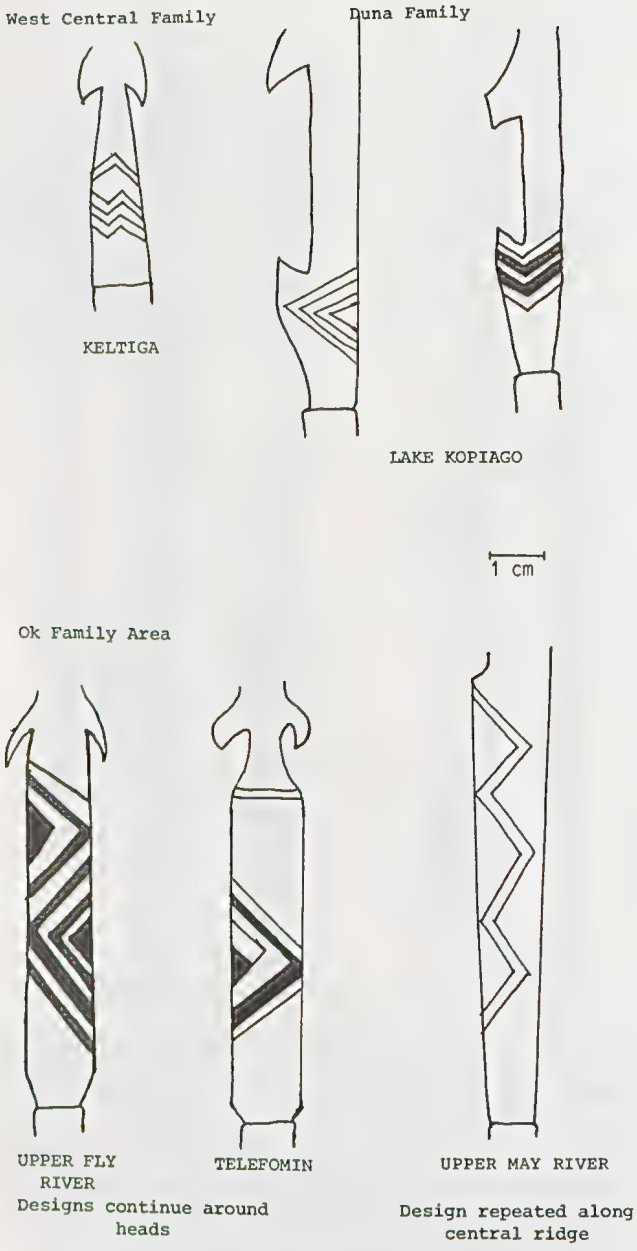


Fig. 33. Designs on heads before barbs commence.

Hourglass (element 10, variant [ii]) is used as on Mendi arrows. From two sources (Wagner, 1967; Hughes, 1971), Karimui trade and conflict appear to be oriented in a south-westerly direction — fighting with the Baria, Miru speakers of Pangia sub-district; trading with the Kewa speakers of Ialibu sub-district, and north with the Chimbu and sout-east Wahgi peoples. thus, the similarities in design patterns on arrows of the Karimui people and the Kewa of the southern part of West Central family area are most probably the result of contact through trade.

Any interpretation of the meaning of elements and motifs in design patterns on traditional highlands' arrows must be speculation, as its significance to the person who made it and the person examining it will be different (cf. White, 1967a). With an iconic analysis, one is dealing with the results of the artist's thought processes manifested in the designs he carved. On only two occasions was I told the meaning of a design and, since this information did not come from the artist, it must be suspect.

However, the occurrence of the ocular or 'eye' element (element 2) on so many traditional arrows seems to indicate that it is intended a realistic element. Variants are recognised by New Guineans as eyes — 'him (arrow) see to fly' — and are commonly found in designs on fighting arrows to ensure they hit their target.

CONCLUSION

My study of Papua New Guinea highlands arrows shows that morphological attributes of arrows can be formally described, and carved designs on heads and fore-shafts can be analysed into elements which in turn may be further analysed into variant forms. The arrows manifest uniformity in component parts with diversity in carved designs, and the main factor responsible for the distribution of arrow design elements, motifs and patterns is the highlander himself.

Highlands arrow design patterns demonstrate regional variations within linguistic boundaries and between linguistic groups, but the within family differentiation is not so great as that between language families. In the distribution of design elements, patterns of association emerge within arrow populations, and some combinations only occur in particular areas. Thus, the geographic distribution of the combination of element 2 'eye' variants with element 9 'heart' variant, points to some link between the northern part of West Central family area and Ok family area across the Strickland Gorge (Fig. 29).

As a result of this study, I suggest that the Chimbu-Asaro physiographic boundary is not a barrier to the interchange of cultural traits, but that there does exist a boundary further westward, running roughly north to south, from the Yuat River to Mt Hagen and the Kaugel River. It is on either side of this boundary that variation of arrow forms and decoration is most clearly visible. I base this statement not on one aspect of the arrows, but several. These are: length, where noticeable differences in the mean occur to the east and west of this line (Table 4); the ratio of carved heads to carved fore-shafts, which shows a distinct reversal at this boundary (Fig. 7); design element distribution, which indicates the use of few to the east and many to the west (Table 9); design patterns, which are more complex and show distinctly different use of elements with deep carving the norm to the west, as opposed to simple designs, light to medium carved to the east; binding type distribution, which shows numerically fewer types west of this line (Table 3).

Linguists have already recognised a language boundary (the western border of Central family) that almost corresponds to the physiographic and cultural

one I postulate, but has it a deeper significance than already indicated by Würm (1975)?

With regard to the Chimbu–Asaro divide, I would like other researchers, whose work involves studies within the highlands of Papua New Guinea, to look again at their results to see if there is any correspondence between my findings and their conclusions.

ACKNOWLEDGEMENTS. The work reported here is part of my M.A. thesis 'Form and Decoration of New Guinea Highlands Arrows' data for which I collected in the field at various locations in the Highlands in 1974, and from museum and private collections in Australia and Papua New Guinea 1974–75. This publication differs from the original thesis in some respects as a thorough re-checking of data indicated adjustments should be made to some results and conclusions.

In my thesis I have acknowledged my indebtedness to all those people who so readily gave me assistance during my field-work and later research. For further assistance in this present work I must re-affirm my grateful thanks to Jim Specht, Peter White and Richard Wright for their encouragement, advice, valuable comments and helpful suggestions.

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Biremia ambocerca n. gen., n. sp., the First Record of the Marine Isopod Crustacean Family Bathynataliidae from Australian Waters

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ABSTRACT. *Biremia ambocerca* n. gen., n. sp. is described and figured; it is distinguished from other bathynataliid genera by lacking operculate first pleopods, and in having biramous uropods. The genus is unique within the Isopoda in having a second endite on the maxilliped. The single specimen was taken off Lady Elliot Island, southern Great Barrier Reef, and is the first record of the family from beyond the south-western Indian Ocean. A new family diagnosis is provided, and a key is given for the 3 monotypic genera of the Bathynataliidae.

BRUCE, N.L., 1985. *Biremia ambocerca* n. gen., n. sp., the first record of the marine isopod crustacean family Bathynataliidae from Australian waters. Records of the Australian Museum 37(5): 295–299.

KEYWORDS: taxonomy, marine Isopoda, Bathynataliidae, Great Barrier Reef.

The family Bathynataliidae Kensley, 1978 was previously known from two monotypic genera recorded only from South Africa (Kensley, 1978, 1979). The occurrence of the family in eastern Australia greatly expands its known range. There are many morphological difference between the Australian specimen and the South African genera, and a new genus is established to accommodate the species. The new genus differs from the other genera in possessing a second endite on the maxilliped, pleonite 1 not visible in dorsal view and uropods with reduced rami. The family diagnosis is here emended.

Family Bathynataliidae Kensley, 1978

Diagnosis. Body dorsoventrally flattened. Cephalon, anterolateral margins expanded; posterior margin fused with pereonite 1. Pereonites 2 to 7 distinct, coxae present on at least pereonites 2 to 6. Pleon with 4 or 5 visible pleonites and large pleotelson; at least 2 pleonites with free lateral margins. Mandible with molar process absent (*Bathynatalia, Biremia* n. gen.) or vestigial (*Naudea*), lacinia present on left (*Biremia* n. gen., *Naudea*) or right (*Bathynatalia*) mandible. Maxillule with 10 or 11 stout spines. Maxilla, inner ramus uni- or bilobed. Maxilliped palp 3-articled, endite with distinct basal suture and single large coupling hook. Pereopod 1 robust, subchelate; pereopods 2 to 6 or 2 to 7 slender. Pleopods lying in chamber formed by thickening of ventrolateral margins of pleotelson; pleopods 1 to 3 with large peduncles, rami setose; pleopods 4 and 5 with small peduncles, rami setation reduced. Uropod insertion subterminal, rami small (smaller than peduncle) or absent.

Type-species. *Bathynatalia gilchristi* Barnard, 1957.

Remarks. The family Bathynataliidae now consists of three genera: *Bathynatalia* Barnard, 1957, *Naudea* Kensley, 1979 and *Biremia* n. gen. As indicated by Kensley (1978, 1979) the family is most closely allied to the Serolidae. The serolid genus *Basserolis* Poore, 1985 further emphasises the similarity of the two families. *Basserolis*, whilst having reduced mouthparts that differ markedly to those of *Serolis* (see Harrison & Poore, 1984), has pereopods and pleopods that are essentially the same as those of *Biremia*.

All serolid genera are easily identified by the fourth pair of pleopods being operculate (Harrison & Poore, 1984; Poore, 1985). In the Bathynatalidae the pleopods are all lamelliform, or the first pair is operculate. In *Biremia* there is an abrupt change in the morphology of pleopods 1 to 3 and 4 and 5, with pleopods 4 and 5 being larger and broader than 1 to 3, a condition approaching that shown by the serolids. Most serolids have a pleon of 3 visible segments and the uropods

lateral in position. However, in *Serolis elliptica* Sheppard, and *Serolis scythei* Lütken (see Moreira, 1974, 1977) the uropods are subterminal, a position similar to that found in bathynataliids. The monotypic serolid genus *Ceratoserolis* Cals has uniramous uropods, while some species of *Serolis* have reduced rami (Menzies, 1962), again a condition similar to that of bathynataliids.

Characters which separate the two families are: pleopods 1 to 3 separated by pleonal tergites in serolids, while in bathynataliids they are mutually adjacent; pleopods laterally enclosed by the pleotelson in the bathynataliids, in serolids they are unenclosed; and mouth parts in the bathynataliids having a large mushroom shaped coupling hook on the maxilliped endite and a large lacinia, both of these being absent from serolids.

Key to Genera of Bathynataliidae

1. Pleopod 1 lamelliform ..... *Biremia* n. gen.

——Pleopod 1 operculate, indurate 2

2. Pereonite 7 with free lateral margins and coxae ..... *Bathynatalia*

——Pereonite 7 without free lateral margins and coxae ..... *Naudea*

Biremia n. gen.

Diagnosis. Pereonite 7 small, lateral margins overlapped by pereonite 6. Pleonite 1 not visible; pleonites 3 and 4 with free lateral margins. Maxilliped with second endite. Pereopod 7 present. Uropods biramous, with reduced rami.

Type-species. *Biremia ambocerca* n. sp.

Etymology. The name is derived from the Latin word *remus* (oar) combine with the prefix *bi-*, and alludes to the biramous uropods. Gender is feminine.

Remarks. The genus is easily distinguished from others in the family by the first pair of pleopods not being operculate and indurated, in having biramous uropods and in being the only genus with eyes.

Of the other two genera *Biremia* is most similar to *Naudea* in somatic morphology, both genera being similar in appearance to serolids. *Bathynatalia* differs from *Biremia* and *Naudea* in having a nodulose body surface and strongly produced acute coxae. Both *Bathynatalia* and *Naudea* share the apomorphic characters of operculate first pleopods, uniramous uropods and lack of eyes. In *Biremia* these characters show the plesiomorphic condition. It is apparent therefore that *Biremia* occupies a place apart within the family.

The single specimen of *Biremia* was taken at a depth of 150 m, substantially shallower than the other two genera which have been recorded from depths between 800 and 900 m (Kensley, 1978, 1979).

Biremia ambocerca n. sp.

Figs 1-3

Type-material. HOLOTYPE, female, 5.0 mm, northeast of Lady Elliot Island, Bunker Group, Great Barrier Reef, 24°03.7'S, 152°49.4'E, 4 July 1984, depth 150 m, rubble bottom with many disc corals, coll. P.H. Coleman, G. Hangay and S. Keable on H.M.A.S. Kimbla (AM P35697).

Description. Body about 1.3 times as long as wide; widest at pereonites 2 and 3. Cephalon with eyes at posterolateral angles. Pereonites 2 to 4 with median dorsal tubercle near posterior margin of segments; pereonites 5 and 6 short, less than half length of pereonite 4; pereonite 7 almost entirely concealed by pereonite 6. Pleon short, about 10% of total body length. Pleonite 1 not visible, pleonites 2 and 3 fused medially, pleonite 4 with median tubercle; pleonite 5 very short, narrower than anterior margin of pleotelson. Pleotelson slightly longer than wide, anterior two thirds with 7 longitudinal ridges; posterior third abruptly depressed, with 6 longitudinal ridges; posterior margin with 2 subterminal excisions and acute median point.

Antennal peduncle 4-articled, article 2 shorter than 1, article 3 longer than 2, article 4 one third length of article 3, articles 3 and 4 with plumose setae; flagellum with 11 articles, distal 2 articles very small; articles 8–10 each with single aesthetasc. Antenna peduncle article 1 short; articles 4 and 5 subequal in length and longest; flagellum with 10 articles, shorter than peduncle.

Clypeus triangular, anteromedial point produced. Mandible palp article 1 very short, article 2 about 6.5 times longer than 1, article 3 twice as long as 1; right incisor with 5 cusps, left incisor with 4 cusps and transversely broad lacinia with 6 short cusps; both mandibles lack molar process; left mandible spine row with 2 spines, right with 4. Maxillule exopod with 10 stout spines, endopod simple lobe with single small seta. Maxilla entire, exopod and palp each with 2 pectinate spines, endopod with 3 spines. Maxilliped palp article 3 with 2 stout terminal setae; second endite present on dorsal side of basis, with single distal spine.

Pereopod 1 prehensile; dactylus slender, extending to posterior of carpus, base of unguis with prominent slender spine; propodus slightly more than twice as long as wide, palm provided with row of 17 stout spines, simple spines alternating with bifid spines; carpus with 2 spines or posterior margin. Pereopods 2 to 7 similar, all slender, increasing in length from 2 to 6; pereopod 7 shorter and with fewer spines than pereopod 6.

Pleopods 1 to 5 peduncles becoming progressively shorter and narrower. Peduncles 1 to 3 with coupling hooks on medial margins. Pleopod 1 rami narrow; endopod slightly longer than exopod, with 9 plumose setae on lateral and distal margins. Pleopod 2 endopod with 5 plumose setae, exopod with plumose setae along lateral and distal margins. Pleopod 3 endopod tapering to truncate apex with 5 plumose setae, exopod with transverse suture, plumose setae along lateral and distal margins. Pleopod 4 rami basally broad, tapering to apical point; endopod without setae, exopod with

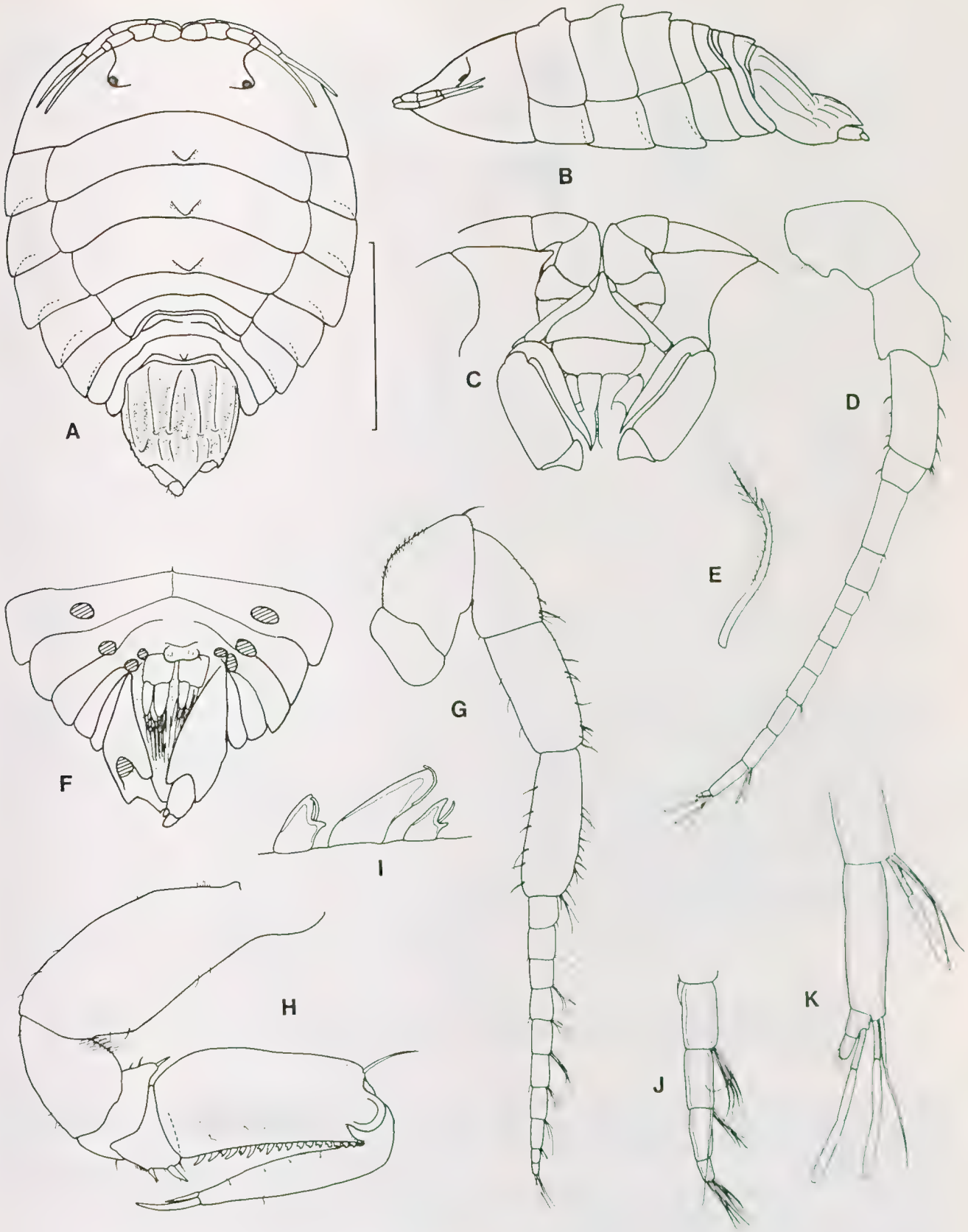

Fig 1. *Biremia ambocerca* n. gen. n. sp., holotype. **A**, dorsal view; **B**, lateral view; **C**, clypeal region; **D**, antennule; **E**, seta from antennule peduncle article 3; **F**, ventral view of posterior pereonites, pleon and pleotelson, showing points of insertion of pereopods and thickened margins of pleotelson; **G**, antenna; **H**, pereopod 1; **I**, spines from pereopod 1 palm; **J**, antennal flagellum, terminal articles; **K**, antennule flagellum, terminal articles. Scale line represents 2.0 mm.

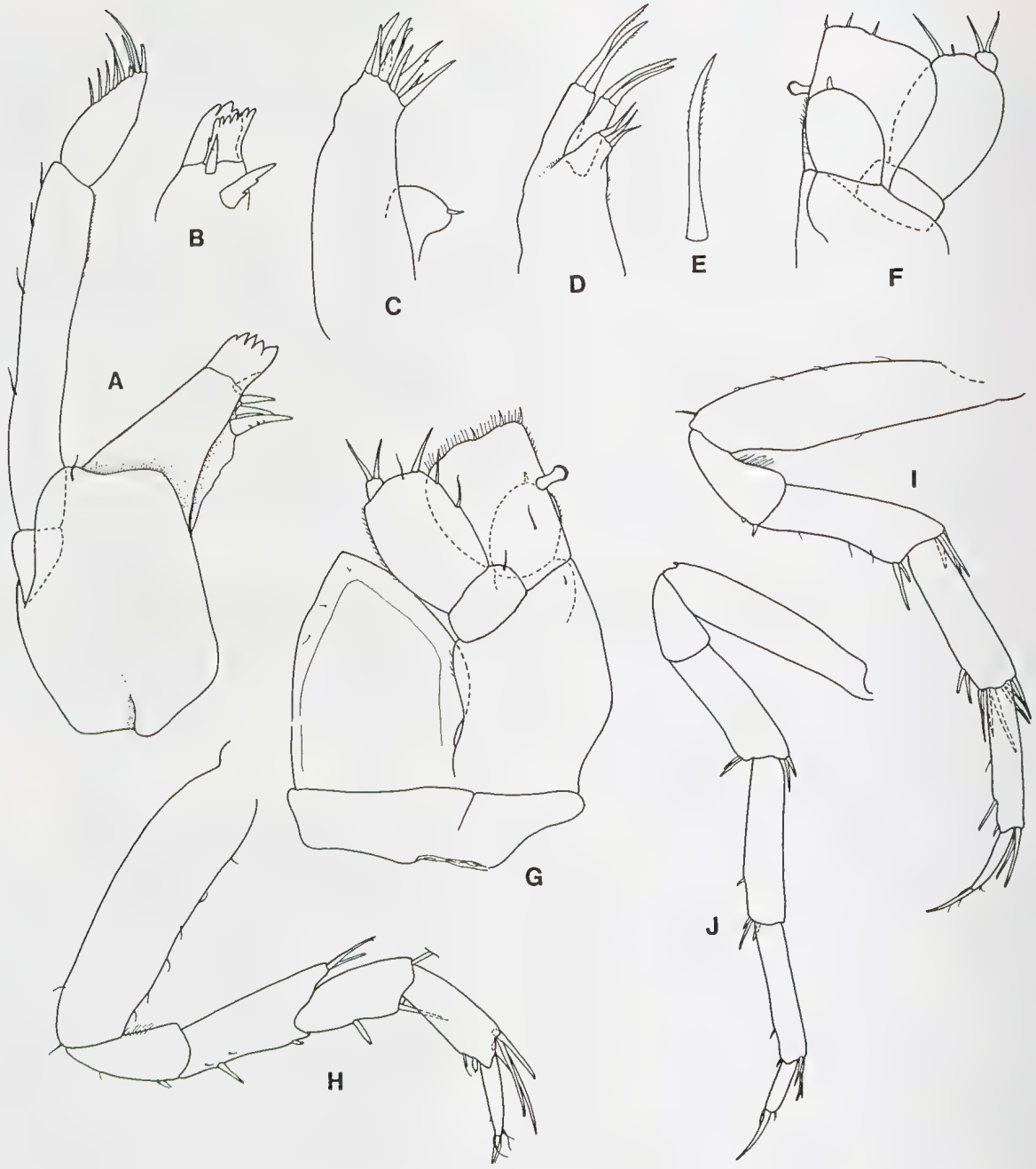

Fig. 2. *Biremia ambocerca* n. gen., n. sp., holotype. **A**, right mandible; **B**, left mandible, incisor, lacinia; **C**, maxillule; **D**, maxilla; **E**, maxilla palp seta; **F**, maxilliped, dorsal aspect; **G**, maxilliped, ventral aspect; **H**, pereopod 2; **I**, pereopod 6; **J**, pereopod 7.

transverse suture and 2 setae on lateral margin. Pleopod 5 similar to 4 but without setae. Uropod peduncle about 3 times as long as wide; rami short, endopod about half as long as exopod.

Etymology. The specific name is derived from the Greek words *ambon* (ridge) and *kerkos* (tail).

Remarks. The shape and sculpture of the pleotelson together with vestigial uropod rami prevents confusion with the other genera and similar looking serolid isopods. The second endite arising from the dorsal side of the maxilliped basis (present on both maxillipeds) is unique within the family, and also appears unique within the Isopoda.

The single specimen of *B. ambocerca* was taken from a sample rich in isopods that included *Serolis* spp., sphaeromatids, *Gnathia* spp. and valviferans.

ACKNOWLEDGEMENTS. This work was completed while in receipt of a Queen's Fellowship in Marine Science.

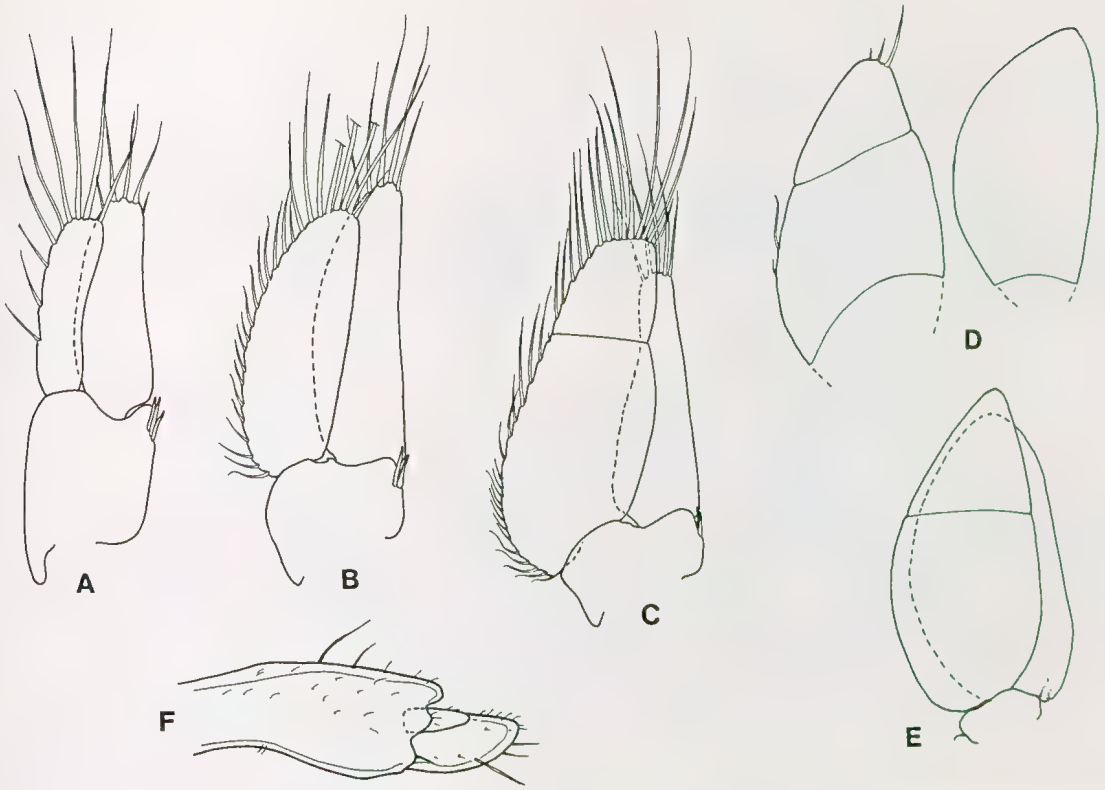

Fig. 3. *Biremia ambocerca* n. gen., n. sp., holotype. **A–E**, pleopods 1–5 respectively; **F**, uropod.

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An Advanced Massive Dipnorhynchid Lungfish from the Early Devonian of New South Wales, Australia

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Abstract. *Dipnorhynchus kurikae* is a large dipnoan of Zlichovian age from limestones at Wee Jasper, New South Wales. Its skull roof is very broad posteriorly, narrow rostrally, has a pineal foramen opening through a single 'D' bone and a small number of bones in front of 'D'. The palatal and mandibular tooth plates are massive. The species is a close relative of *D. sussmilchi*.

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Keywords: Dipnoi, Devonian, evolution, *Dipnorhynchus*.

Several highly significant fossils were found closely associated in the Zlichovian Limestones at Wee Jasper, New South Wales (Fig. 1). Among these were a partial skull roof, palate and mandible of a massive dipnoan. Subsequently another fragment of a skull roof and two partial palates were recovered from the same locality. A similar large mandible had been found at this locality several years previously but it had been regarded as a gerontic individual of *Dipnorhynchus sussmilchi* (Campbell & Barwick, 1983). The skull fragments and three palatal fragments, which are all of comparable dimensions, provide enough data to demonstrate that a more advanced form than *D. sussmilchi* is represented. Using the criteria usually applied in the differentiation of genera and species of Devonian Dipnoi, this material is described as a new species.

SYSTEMATIC PALAEONTOLOGY

Dipnorhynchus kurikae n. sp.

Figs 2–10

The holotype is ANU35674, the posterior part of a skull roof; paratypes ANU35675, 36508–36510 and 36519 are a partial skull roof, three partial palates and a snout respectively; ANU35643 and AMF64832 are partial mandibles. All come from the shore of Burrinjuck Dam, Goodradigbee River (Fig. 1).

The species is named in honour of Dr Elga Mark-Kurik who discovered the first skull roof fragment.

Formation and Age. From the transition between the Bloomfield and *Receptaculites* Limestones, Goodradigbee River, Wee Jasper, N.S.W. One of the specimens occurs about 10 m higher in the section than the others, and is within the *Receptaculites* Limestone. Zlichovian.

Diagnosis. Large species. Width to length ratio of skull high, this ratio for the palate being ca. 1.5. Large 'K' not extending between 'X' and 'L'. 'I' bones meeting behind 'B'. Pineal foramen open. One to three 'D' bones present. One to three 'L' bones depending on size of 'K'. Bones 'M' and 'N' large. Rostrum narrow. Palate exceptionally thick and transverse across the articular region. Small anterior median palatal bone embraced within paired 'dermopalatines', and all fused to the pterygoids. Dentition consisting of bulbous masses similar to those of *D. sussmilchi*. Dentine thin over most of the palate but thicker on the marginal ridges and the bulbous 'teeth'. Mandible very long medially and with a very powerful symphysis; ratio of median length/total length ca. 0.70. Anterior furrow deep, and divided by a forward extension of the 'adsymphysial' plate, at least in large adults. 'Dentary' very short on the ventral side of the mandible but with long dorsolateral extensions around the anterior furrow. 'Splenials' and 'postsplenials' long and narrow. 'Surangular' deep and long, extending forwards to the anterior end of the labial pit. Massive bulbous tuberosities on the heel of the 'prearticulars' and smaller elongate teeth immediately behind the anterior furrow. Marginal ridge on the dentary continuous with that on the anterior end of the 'prearticulars'. Dentine thicker on the marginal ridges and bulbous teeth than elsewhere.

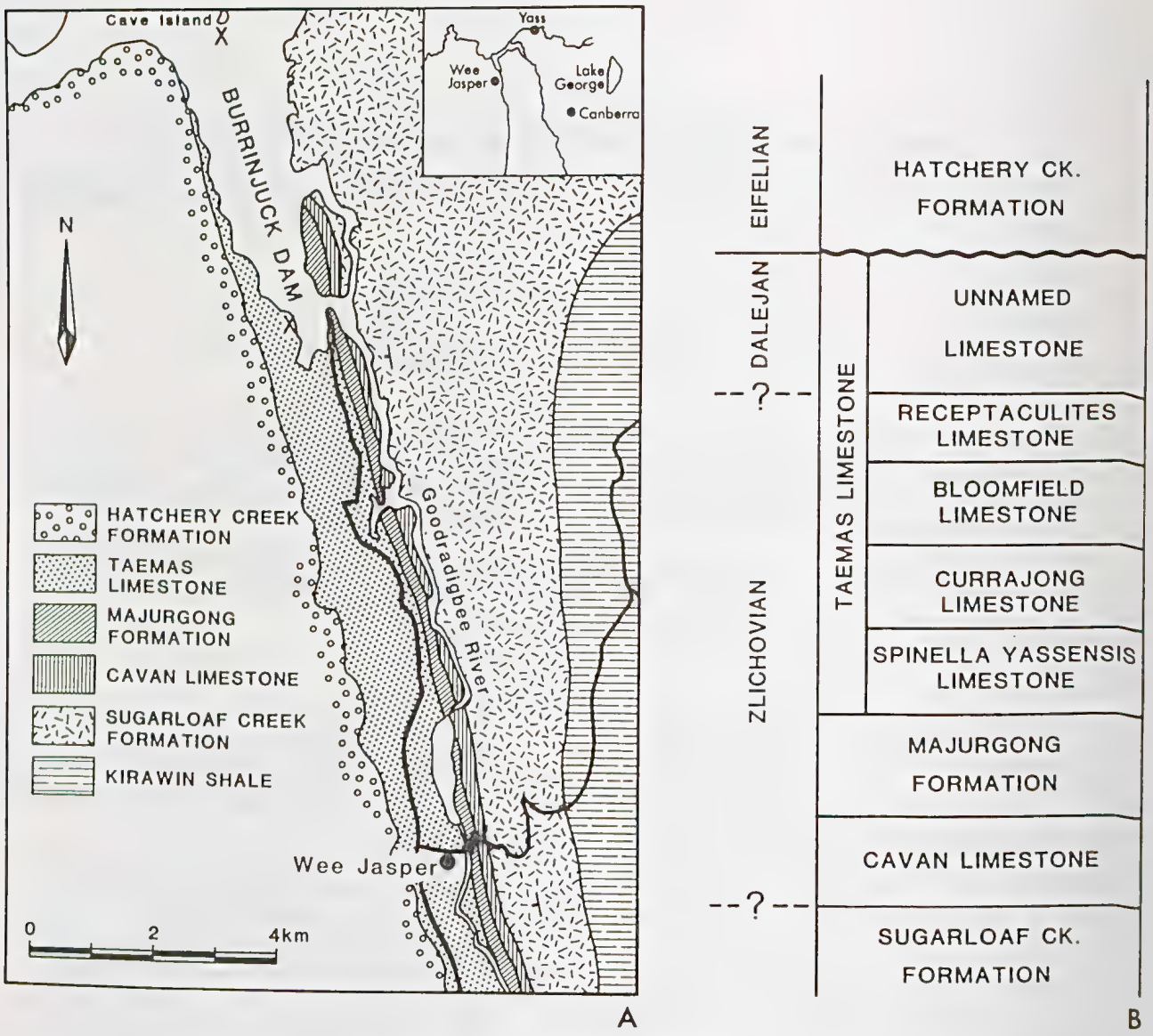

Fig. 1. a, Geological map of the Wee Jasper area, N.S.W. Main collection site marked X; b, subdivisions of the Taemas Formation in the Wee Jasper area.

Comparative Description. The large 'D' with the open pineal foramen in the holotype is unlike the arrangement seen in any other known genus. *Uranolophus wyomingensis* has a comparably large 'D' but no pineal foramen. The paratype ANU35675, with its second and perhaps third 'D' bone, is more like *D. sussmilchi*. The reduction of the number of 'D' bones is a well known feature of dipnoan evolution (Miles, 1977, p.305), and it is clear that *D. kurikae* has advanced well beyond the *sussmilchi* stage in this character.

Bone 'K' is in the primitive position relative to 'X' and 'C', but it is very variable in size. In ANU35675 it is comparable in size with the bone 'K' in *D. sussmilchi*, but in the holotype it is greatly expanded, particularly on the left side where it occupies the space of bone 'L_1' as well as 'K'. In this respect it should be noticed that the type of *Speonesydrion lehmanni* (Campbell & Barwick, 1984b) and some variants of *Uranolophus wyomingensis* have a comparably large bone in this position (Denison, 1968, fig. 3).

The lateral line canal from 'J' passes directly to 'K' and the radiographs of ANU35675 show no signs of an anastomosis with the canal in 'X'. Bone 'X' is massive, and proportionately wider than the equivalent in any other species. Bone 'L_2' also is unusually large, and on the left side of the holotype it is enormous. The 'I' bones are very transverse and their ossification centres are posteriorly placed.

Part of a snout has already been illustrated (Campbell & Barwick, 1984a, fig. 6). This is well ossified and has

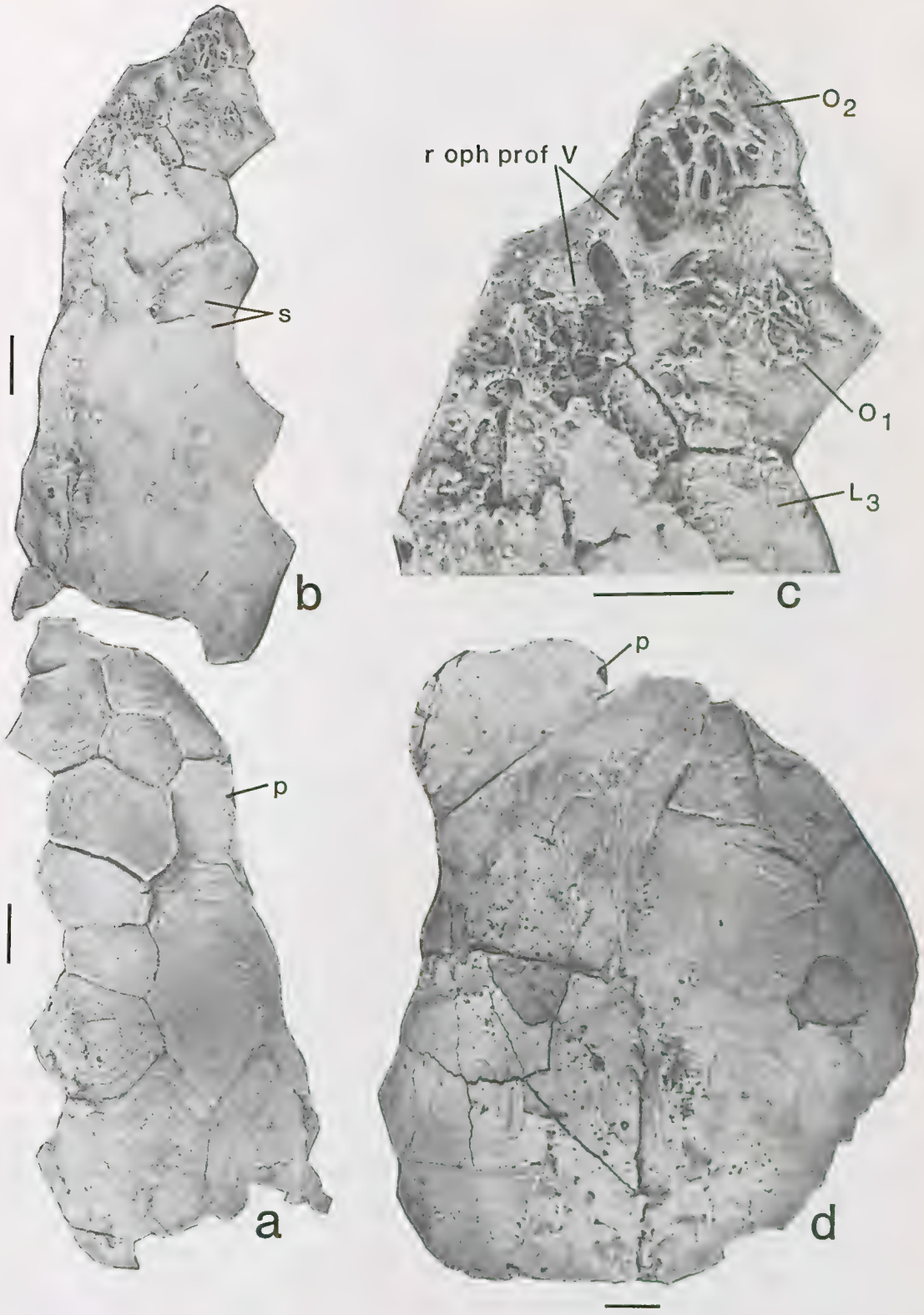

Fig. 2. a, b, Skull roof of ANU35675 in dorsal and ventral views respectively. The specimen is slightly humped and twisted medially as a result of tectonic distortion; c, enlargement of the canals in the ethmoid capsule of the same specimen; d, the holotype roof. p = pineal foramen; r oph prof V = ramus ophthalmicus profundus V; s = encrusting serpulid worms; L_3, O_1, O_2 = dermal roofing bones. Scales = 10 mm.

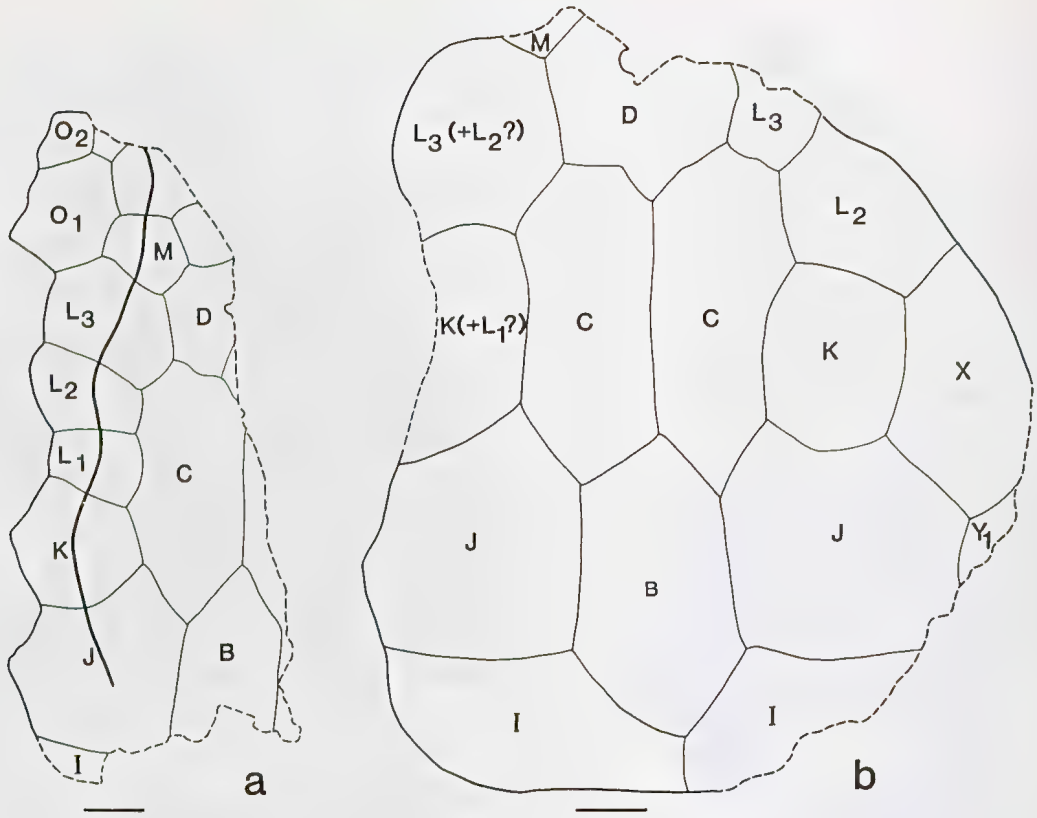

Fig. 3. Interpretation of the two skull roofs shown in Figure 2. The lateral line canals in ANU 35675 have been located from X-radiographs. Scales = 10 mm.

numerous perforations associated with the lateral line and rostral tubule systems. It also is a narrow structure, which makes it easy to distinguish from the much broader snouted *Speonesydrion iani* with which it occurs.

The number of bones anterior to 'D' cannot be determined from the available specimens, but judging from ANU35675 in which the single large 'N' extends well towards the mid-line and the bone immediately in front of 'D' is large, the number of bones must be less than in *D. sussmilchi* and *D. kiandrensis*. Bone '3' must have been very large on the fragment ANU35675, as is shown on the reconstruction on the left side of Figure 4. There it is in contact with 'K', an unusual feature which is also found on one side of the holotype of *D. sussmilchi*. Thus the skull roof shows a mixture of advanced and primitive characters.

A few tubules from the ethmoid capsule are preserved under the rostral region of ANU35675. Two very large interconnected tubes are present medially. From their position relative to the lateral line canal and the roofing bones, they can be homologised with canals connected with the medial and lateral branches of the profundus nerve. A fragment of what is probably part of the superficial ophthalmic canal is present marginally. All these tubules are interconnected and they ramify towards the dermal bones as described previously in *D. kiandrensis*.

The palate is reminiscent of *D. sussmilchi* in overall shape and in the presence of bulbous tuberosities. These become disproportionately massive in large specimens. There is a median tuberosity at the anterior end of each pterygoid and this was probably contiguous with a smaller tuberosity on the anterior median plate, as in *D. sussmilchi*. The marginal ridge is weakest posteriorly and extends forwards to the anterior end of the pterygoid where it forms a semi-isolated elongate 'tooth'. Posterolaterally on each pterygoid there is a broad concave surface that occludes with the main tuberosities on the mandible. Between these surfaces on the smaller specimens is a flat low eminence, but on the largest individual, ANU36510, the eminence is massive and transverse. This leaves a deeply concave medial surface on the palate as a whole (Fig. 5). The dentine is thin over the concave surfaces but more than doubles its thickness on the tuberosities (Fig. 6). Nevertheless it is clear that the prominences on the palate are largely formed of bone with relatively thin dentine surfaces.

The dentine is not well preserved, but on the tuberosities it is of the same type as that found on the heels of the tooth plates in *Speonesydrion* (Campbell & Barwick, 1983, fig. 12). On all four specimens of the palate available, the dentine on the flat or concave surfaces consists of two distinct layers. The outer layer is less than 1 mm thick and consists of heavily mineralised tissue with almost completely occluded pulp

canals. It cracked easily during preservation, and while being prepared it tended to peel away cleanly from the underlying tissue. This consists of uniform vertical pulp canals ca. 0.07–0.12 mm in diameter, and is clearly distinguished from the underlying coarser bone. The preservation does not permit the recognition of circumpulpal or interstitial dentine if such were present.

Cross sections at various positions through the palate show no sign of sutures between the pterygoids or between the pterygoids and the parasphenoid. However, the dermal palatal bones thicken considerably towards the mid-line where they form a pronounced ridge supporting the base of the neurocranium (Fig. 6d). This same figure clearly shows the extent of the neurocranium on the floor of the anterior part of the orbital chamber, the boundary between the dermal and neurocranial bone being very sharply defined. The extent of the canal system traversing the neurocranial bone is also well seen (cf. Campbell & Barwick, 1982a, fig. 16; 1984b, fig. 9B, for similar structures in *D. sussmilchi* and *S. iani*).

The hypophysial stalk is long and thin (Fig. 6e) and opens through a small foramen near the posterior end of the palate. It is inclined at an angle of ca. 40° to the palatal surface. The palatine nerves and arteries leave the hypophysial pit in the same manner as in other Early Devonian dipnoans.

As in all these primitive genera in which dentine covers the whole palatal surface, the limits of the parasphenoid on the palatal surface cannot be observed, but it is assumed that the hypophysial stalk lay approximately parallel to the anterior edge of the parasphenoid as it does in *Chirodipterus australis* (see Campbell & Barwick, 1982a, figs 6a–d). Cross sections do not show any sign of a suture between the parasphenoid and the pterygoids, but the bone structure of the parasphenoid is coarser than that of the pterygoids (see Fig. 6c, e). The posterior face of ANU36508 shows the coarsely vesicular bone of the parasphenoid, and the distinctive structure of the bone that lies immediately beneath the dentine covering its ventral surface (see below). The posterior part of the parasphenoid is not preserved completely but what there is of it resembles the equivalent part of *D. sussmilchi*.

The quadrate is a massive bone and stands almost vertically. Its front wall is heavily dimpled, presumably for the attachment of muscles. On ANU36510 the whole of the unfinished surface occupied by the articulatory cartilage pad in life, is beautifully preserved. The cartilage must have been extremely thick, and acted as a resilient stress-bearing tissue to resist the forces of the massive bite. Its outline clearly shows a narrowing and slight protrusion of the lateral part of the surface to match the form of the glenoid fossa.

On the medial side of the articulatory surface is an enormous striated area for the attachment of the pterygoid-mandibular ligament. This is so large a structure that the pterygoid has developed a special process to carry it in ANU36510 the largest specimen, though in ANU36509 no such process is present.

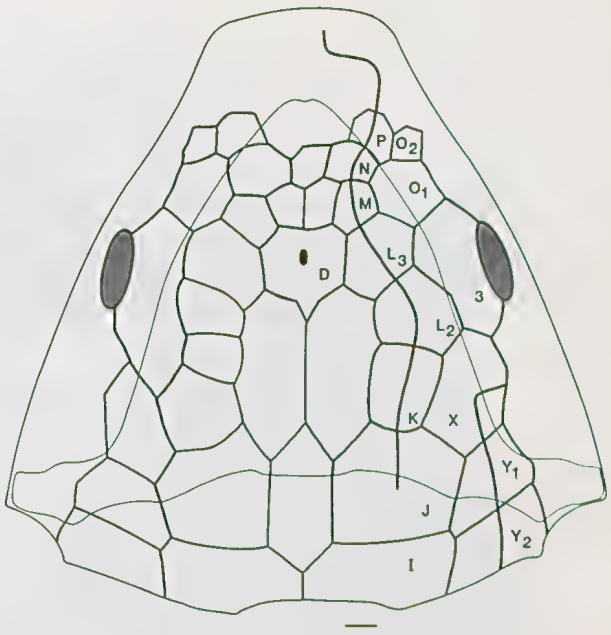

Fig. 4. Reconstruction of a dorsal view of the skull of *Dipnorhynchus kurikae* with the outline of a palate beneath. The left side of the roof is modelled on ANU35675 and the right side on the holotype. A single bone 'D' is figured as in the holotype. The roof anterolateral to 'D' is known only on the former specimen, and hence the right side reflects that same individual. Bone 'P' has been restored from the preserved fragment and the location of its centre fixed by projecting the lateral line canal in 'N'. Bones '3' are outlined from what is known of their inner edges, and the postion of the orbits in *D. sussmilchi*. The sizes of bones 'Y_1' and 'Y_2' are inferred from a restoration of the skull width by superimposing the outline of the palate on the roofing pattern; they could be somewhat wider than shown. The width of the snout is inferred from a single fragment, the position of 0_1 and 0_2, which limits the width in that region, and the superposition of a mandible, the dentary of which should fit neatly between the ends of the subnasal ridges. No attempt has been made to restore the cheeks. Scale = 10 mm.

In the angle between the parasphenoid and the pterygoid is a deep triangular pyramidal pit, similar to that described for *D. sussmilchi* (see Figs 5c, 7). Specimen ANU36510 is so large, and the foramina associated with this pit are so clear, that it is possible to clarify some of the points related to this structure. It has three canals leading into it from the posterior, two into its apex and the other into its ventromedial side. Of the two opening into the apex, the more lateral one is a continuation of a groove across the posterior face of the quadrate, running off that bone behind the jaw articulation. A similar groove occurs in *D. sussmilchi* where it has been interpreted as the r. mentalis externus VII. The more medial of the two apical openings connects with a groove that runs around the edge of the parasphenoid, and is interpreted as being for the internal carotid artery. The third (medial) opening is also connected with this groove. The canal into which the foramen opens cannot be traced with certainty, but it has an anterodorsomedial orientation. At present it can be identified only as a branch of the internal carotid artery.

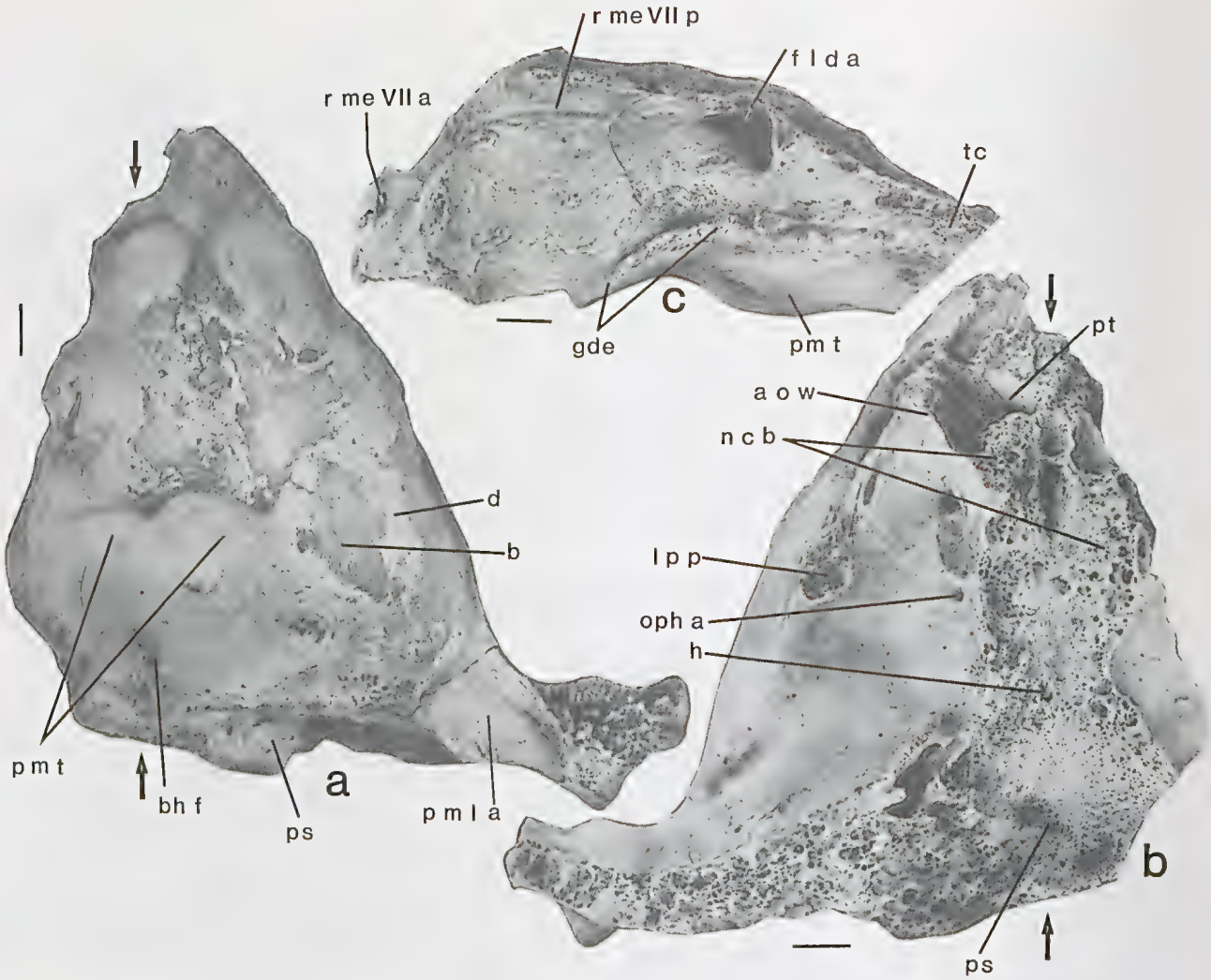

Fig. 5. The largest known palate of the species ANU36510 in ventral, dorsal and posterolateral views. In (a) note the patchy preservation of the thin superficial dentine layer which splits and peels away to expose a basal layer with vertical canals of uniform size as shown on Figure 6b. The lineations in the region marked 'b' are growth lines. This part of the palate occludes with the massive tuberosities on the mandible. a o w = antorbital wall; b = pterygoid bone showing growth lineations; bh f = buccohypophysial foramen; d = superficial dentine layer; f l d a = foramina for lateral dorsal aorta; gde = growing dentine edge; h = hypophysial stalk; l p p = lateral palatal process; n c b = neurocranial bone; p m l a = pterygoid mandibular ligament attachment; pm t = posteromedian palatal tuberosity; ps = parasphenoid; pt = pterygoid; r me VII a and p = foramina and grooves for anterior and posterior rami of the mandibularis externus VII; tc = encrusting tabulate coral *Syringopora*.

Specimen ANU35610 shows one important feature not previously recognised in a dipnorhynchid. The outer extremity of the quadrate above the jaw articulation is preserved, and it carries a canal through from the posterior face to open anterior to the jaw articulation, precisely as does the canal interpreted as carrying the r. mentalis externus VII in *Chirodipterus australis* (see Miles, 1977, figs 34, 35, 37). The groove on the posterior face of the quadrate leading to this canal is incomplete, but it clearly lay dorsal to the groove interpreted above as carrying the r. mentalis externus VII. This information makes possible a reinterpretation of the facialis branches in *D. sussmilchi* given by Campbell & Barwick (1982a, figs 11, 12). The groove labelled 'r. hyomandibularis VII' must be one division of the mentalis externus branch of that nerve, and the one labelled 'mentalis externus VII' is a second anterior branch of the same nerve. We reach this conclusion because the latter branch clearly passes behind the articulation to enter the mandible from a posterior direction at a small foramen labelled 'f me VII p'. Only a nerve can follow such a course and judging from *Neoceratodus forsteri*, the only possible nerve is the r. mentalis externus VII. The r. mentalis internus VII follows a more ventral course.

The mandible is a massive structure (see Table 1). It

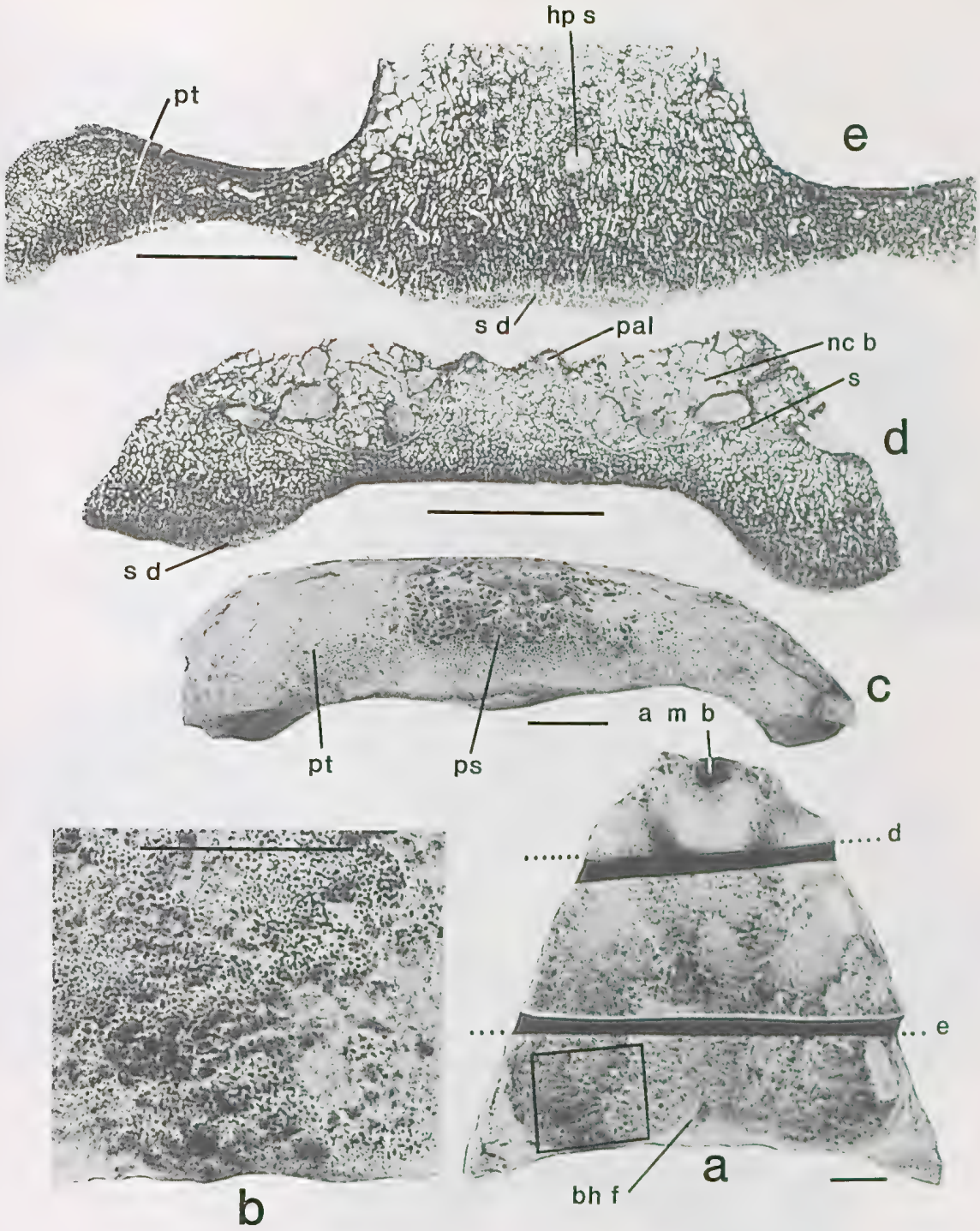

Fig. 6. a, The palate of a small specimen ANU36508 from which most of the surface layer of dentine has been removed except on the tuberosities. The two 'dermopalatines' and the anterior median bone have been lost, leaving rough bone edges; b, enlargement of the posterior part of the palate indicated on (a). Note the regular pattern of fine canals; c, posterior view of the same specimen showing the coarsely vesicular bone of the parasphenoid contrasted against the denser bone of the pterygoids and tissue of the palatal covering with its very fine canals; d, and e, thin sections taken from the positions shown on (a). In (d) note the sharp division between the canal-bearing vesicular neurocranial bone and the much denser pterygoids, the absence of a suture between the two pterygoids, and the thickening of the dentine on the tuberosities. This section was cut before the specimen was etched from the matrix and hence the cavities are filled with carbonate. Section (e) was cut after etching. In (e) note the narrow hypophysial stalk, the coarsely vesicular bone in the upper part of the parasphenoid, the continuity of the even textured bone across the palatal surface and the absence of any sutures bounding the parasphenoid. a m b = space for anterior median bone; bh f = buccohypophysial opening; hp s = hypophysial stalk; nc b = neurocranial bone; pal = palatine nerve; ps = parasphenoid; pt = pterygoid; s = suture between neurocranium and pterygoid; s d = superficial dentine layer on medial and anterolateral tuberosities.

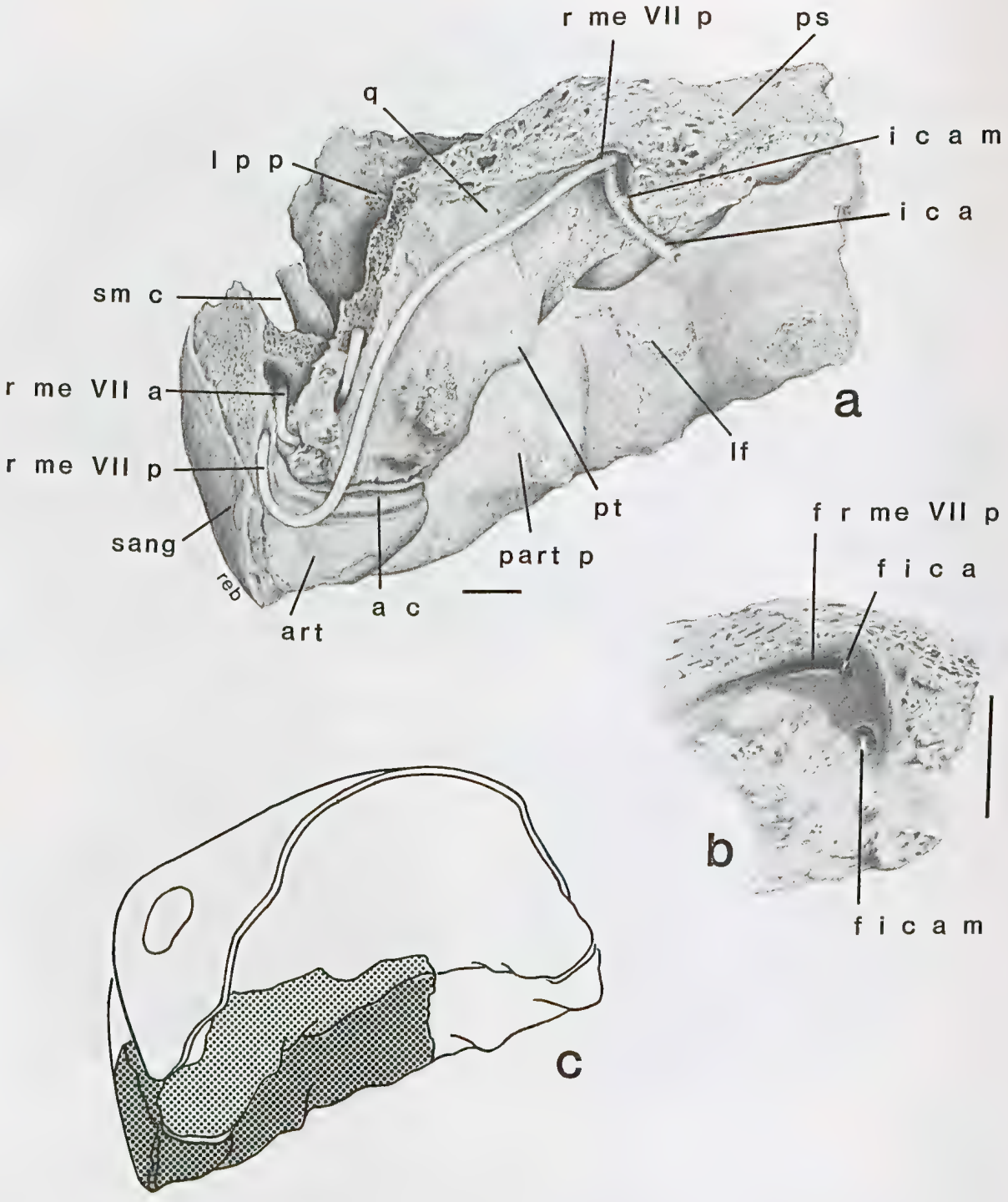

Fig. 7. Reconstruction of the left articular region of a skull and mandible in posterodorsolateral view, based on ANU35610 and AMF64832. a, reconstructed nerves, vessels and foramina; b, enlargement of the complex foramen for the facialis nerve and internal carotid artery to show the several small foramina it encloses; c, outline diagram of posterior face of skull in perspective to show location of Figure 7a. a c = articular cartilage; art = articular; f i c a = foramen for internal carotid artery; f i c a m = foramen for internal carotid artery, medial branch; f r me VII p = foramen for the ramus mentalis externus VII, posterior branch; i c a = internal carotid artery; i c a m = internal carotid artery, median branch; l f = lingual furrow; l p p = lateral palatal process; part p = prearticular process; ps = parasphenoid; pt = pterygoid; q = quadrate; r me VII a and p = ramus mentalis externus VII anterior and posterior; sang = surangular; sm c = suprameckelian cavity. Scales = 10 mm.

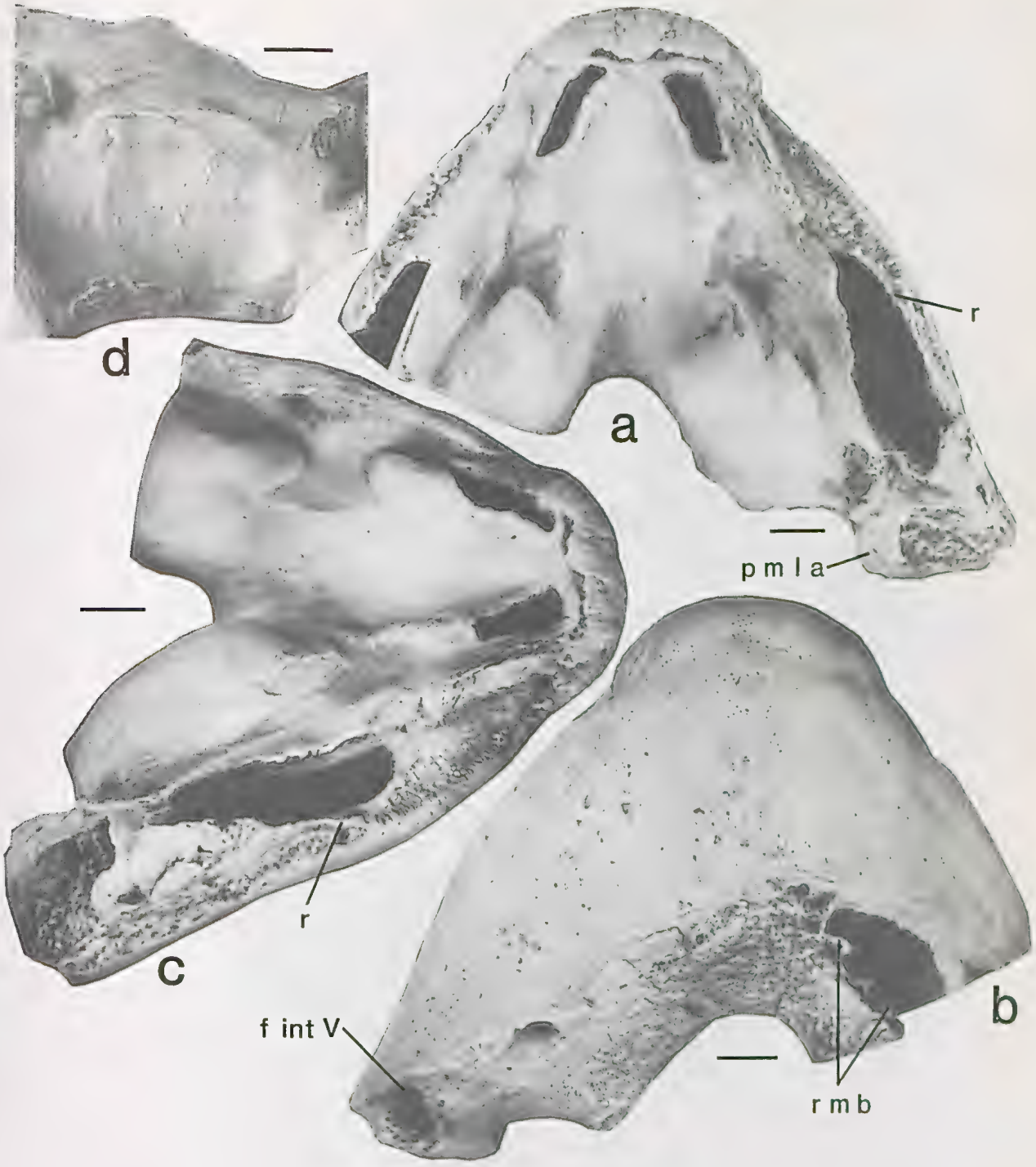

Fig. 8. a, Dorsal, b, ventral and c, oblique view of ANU35643; d, posteromedial view of the right 'prearticular' tuberosity showing the composite nature of the structure with its three surfaces at slightly different levels, the anterior one being the highest. p m l a = pterygoid mandibular ligament attachment; r = ridge separating the vertical and horizontal parts of the dorsal lamina on the 'surangular'; f int v = foramen for ramus intermandibularis V; r m b = ridges on Meckelian bone lining the prearticular face of the Meckelian cavity. Scales = 10 mm.

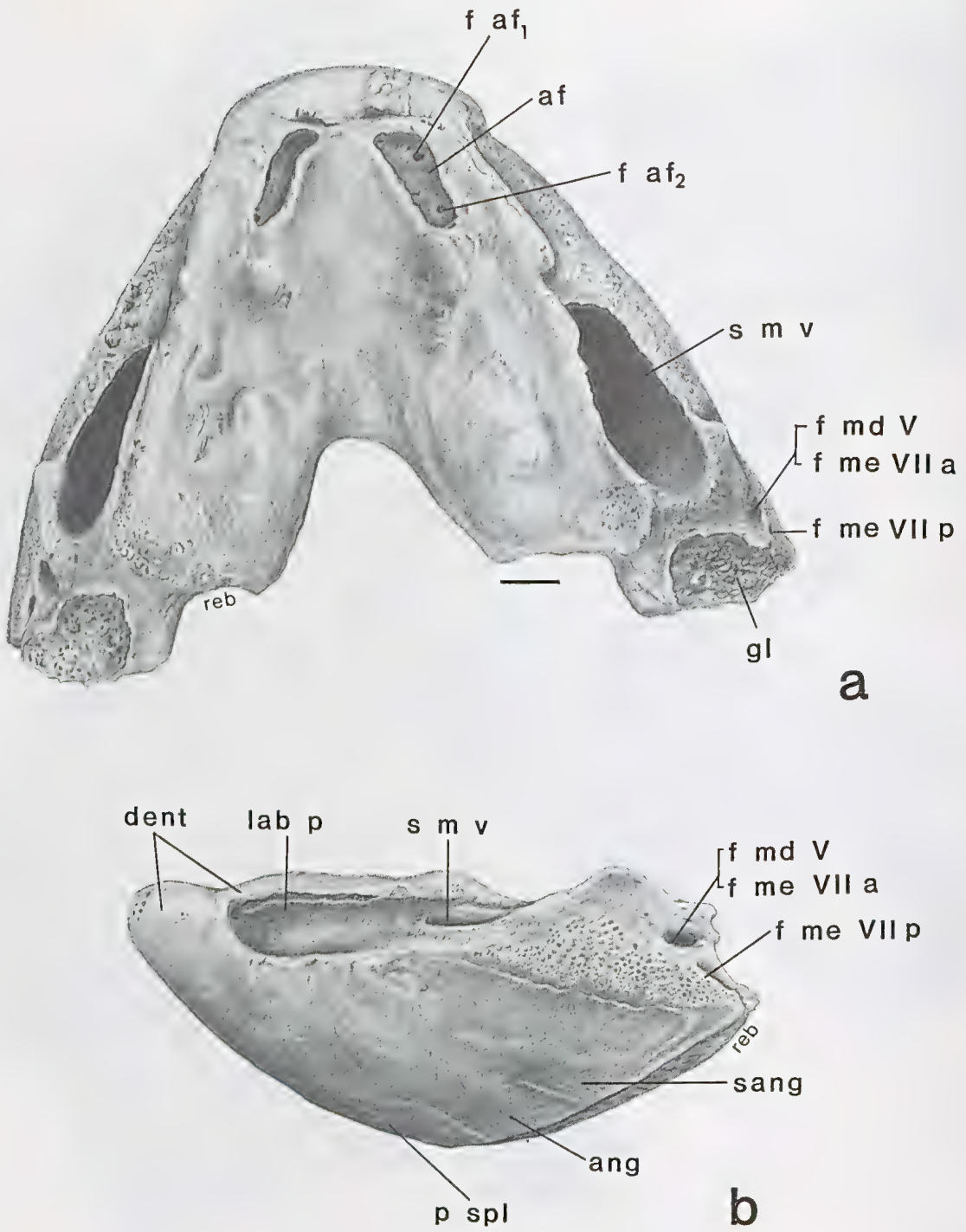

Fig. 9. Reconstruction of the mandible based on ANU35643 and AMF64832 to show details of the labial pit, the anterior furrow, the dorsal surface of the surangular and the glenoid fossae. a, dorsal view; b, left lateral view. af = anterior furrow; ang = angular; dent = dentary; f af_1 and $_2$ = foramina in anterior furrow; f md V = foramen for ramus mandibularis V; f me VII a and p = foramina for ramus mentalis externus VII, anterior and posterior; gl = glenoid fossa; lab p = labial pit; p spl = post splenial; sang = surangular; s m v = supramеckelian vacuity. Scales = 10 mm.

Table 1. Key measurements of skull roof, palates and mandibles in *Dipnorhynchus kurikae* n. sp.

Skull Roof	**ANU35674**	**ANU35675**	
Length from anterior of 'D' to posterior of 'B'	108*	82*	
Palates	**ANU36508**	**ANU36509**	**ANU36510**
Total width across articulation	—	132*	188*
Max. width of dentine bearing surfaces	74	82*	120*
Total length of pterygoids	74	—	120*
Mandibles	**ANU35643**	**AMF64832**	
Total length	92*	—	
Total width	139*	156*	
Symphysial length	66	—	

* estimated values; all dimensions in millimeters

also has been illustrated previously as *D. sussmilchi* (Campbell & Barwick, 1983, figs 4, 6). The specimen from Buchan, Victoria, illustrated by Thomson & Campbell (1971, figs 48–50) probably belongs to this species also. In most respects the mandible is close to that of *D. sussmilchi*, and hence it is not described in detail. The following are the most significant points.

Specimen AMF64832 shows the articulatory region superbly. The foramen previously interpreted as carrying 'r. mandibularis V' in dipnorhynchids certainly has a finished surface across the top of the preglenoid process for the passage of that nerve, and we confirm that interpretation. On the other hand, as shown above, one branch of the 'r. mentalis externus VII' passes in front of the articulation and must have entered this foramen also, exactly as in *Chirodipterus australis*. Other foramina and grooves and canals inside the Meckelian cavity are as in *D. sussmilchi* and *S. iani*.

The Meckelian bone forming the posterior margin of the jaw between the 'prearticular' and the external dermal bones is massive, and is well shown on AMF64832 where its boundaries are enhanced by weathering. It is exposed almost to the mid-line (Fig. 10b).

On the ventral surface the dentary is very short extending back only as far as the anterior end of the labial pits. Its posterior edge is marked by a broad shallow groove. On the dorsal surface it forms a prominent marginal tooth ridge that extends back almost to the anterior end of the suprameckelian vacuity and, as is normal in these primitive genera, it has a relatively sharp contact with the Meckelian bone that forms the floor of the labial pit. Across its dorsal surface in front of the anterior furrow the dentary has a pronounced furrow which at first sight may be thought to define the posterior edge of the bone. Its relation to the adsymphysial plate is obscure though fusion has clearly taken place. The dentary and the adsymphysial plate are approximately on the same level whereas in *D. sussmilchi* the adsymphysial plate is much lower.

The surangular is a deep bone that extends forwards to the anterior end of the labial pit. Posterodorsally it has the usual thin vertical blade covered with cosmine-coated beads. This is separated from its anterodorsal margin by a sharply defined keel in front of which the surface is abruptly inflected forming first the edge of the suprameckelian vacuity and then the floor of the labial pit. This large flat surface has cosmine-coated beads along its outer edge only. The splenial, postsplenial and angular are easily distinguished and are similar to those of *D. sussmilchi*. They are all long bones — much longer than their homologues in *Speonesydrion iani*.

The lateral line canals are deeply buried but their course can be followed by the presence of pores. One interesting feature is that the oral canal does not open posteriorly on the surangular (cf. Miles, 1977, figs 108, 109). The branch of the 'ramus mentalis externus VII' that enters the jaw through the more posterior of the two foramina lateral to the articulation, runs forwards along the inner face of the surangular, and connects with the oral lateral line canal by a row of pores.

The prearticulars have a high marginal ridge where they join the dentary, but this rapidly decreases in height along the inner edge of the suprameckelian vacuity. An elongate tuberosity lies immediately behind the anterior furrow, and a massive tuberosity forms the bulk of the tooth plate surface. These structures are high and well rounded, and the one on the right side of ANU35643, which is preserved entire, is clearly a composite structure (Fig. 8d). To maintain such shapes there must be differential growth from the base, and remodelling of both the bone and the dentine that form the mass of the tuberosity is required. The process by which this takes place requires further study, but presumably it is comparable with the process by which the cushions on the heels of the tooth plates of *Speonesydrion* are produced. This matter, and the nature of the dentine involved are discussed and figured by Campbell & Barwick (1983). Both features are discussed below.

In the floor of the anterior furrow one or two large foramina and several small ones open down into tubules within the symphysial space. A large foramen in its posterior angle leads to a posteriorly directed canal that opens into the Meckelian cavity. Another large foramen in the anterior extremity of the labial pit opens into the symphysial space. In all these features it is a typical dipnorhynchid.

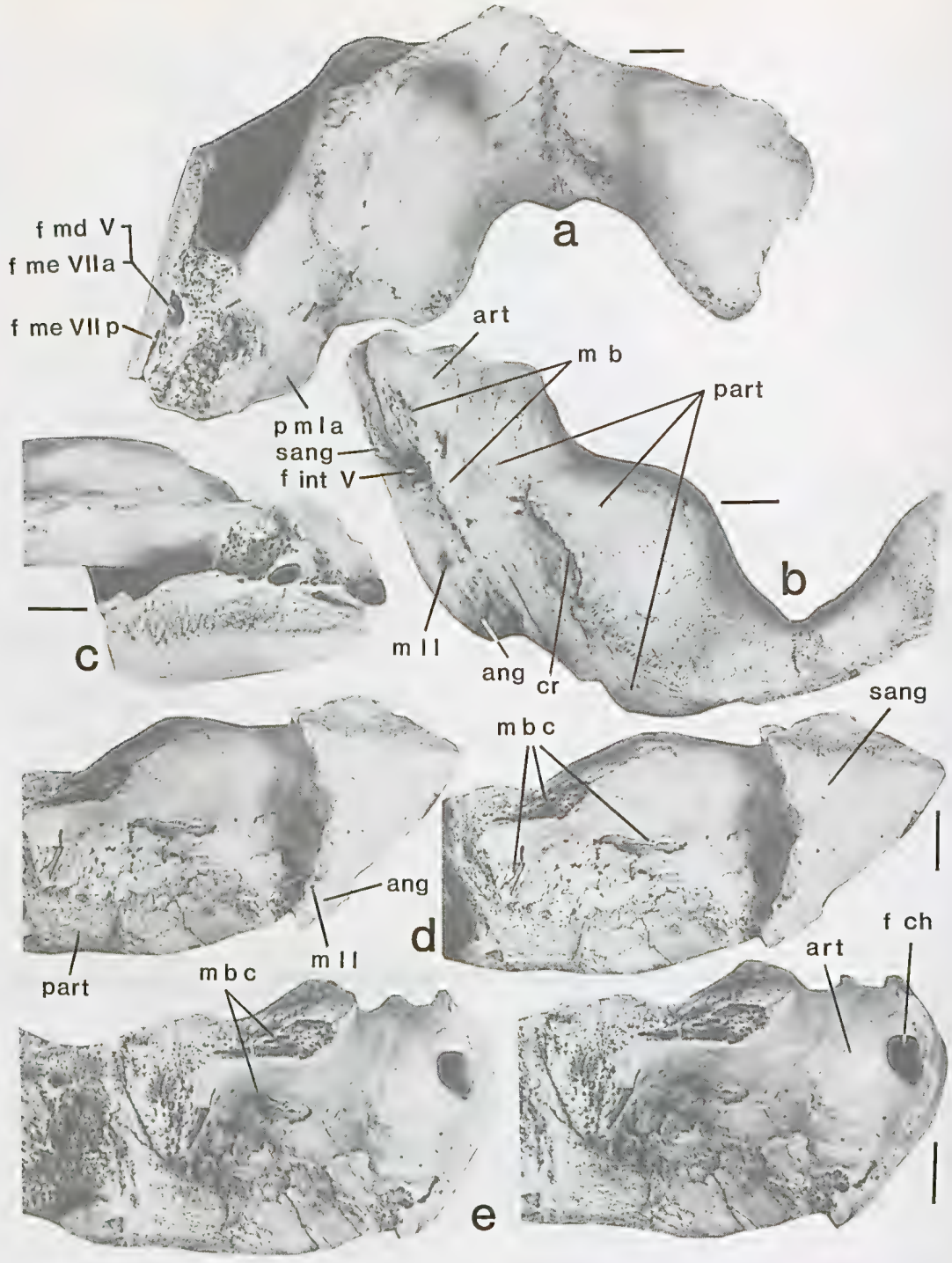

Fig. 10. Several views of the largest known mandible, AMF64832. a, dorsal and b, posterior views. Note the ragged edges of the dentine around the posterior dedges of the tuberosities in (a), and the striations on the prearticular in (b). A large crack separates the main part of the heel of the prearticular from its posterior wall. c, dorsolateral view of part of the left ramus to show the foramina and canals for the r md V and the two branches of r me VII; d, stereopair of a lateral view of the left ramus. Note the vertical blade and the Westoll lines on the 'surangular'. e, stereopair of a view from the anterior into the left Meckelian cavity. Note the thick Meckelian bone lining the floor, inner wall and roof of the cavity, and the numerous canals visible where the bone has been broken. The canals are as in *D. sussmilchi* and *S. iani* (Thomson & Campbell, 1971, figs 21, 22; Campbell & Barwick, 1984b, figs 24, 25). The foramen f ch passes out of the articular separated from the 'surangular' only by a thin sheet of Meckelian bone. ang = angular; art = articular; cr = fracture within the prearticular; f ch = foramen leading to chamber in the articular; f int V = foramen for ramus intermandibularis V; f md V and f me VII a = foramen for ramus mandibularis V and ramus mentalis externus VII, anterior branch; f me VII p = foramen for ramus mentalis externus VII, posterior branch, which runs forwards through f ch immediately inside the oral lateral line canal; m b = meckelian bone; m b c = neurovascular canals in the meckelian bone; m l l = mandibular lateral line; part = prearticular; p m l a = pterygoid-mandibular ligament attachment; sang = surangular.

Summary. *D. kurikae* was a durophagous feeder after the style of *D. sussmilchi*, but it had a much more massive head with an extremely thick palate. The space for the adductores mandibulae was enormous and its bite must have been very powerful. The associated rich marine invertebrate fauna leaves little doubt that like *D. sussmilchi* it fed on hard shelled invertebrates.

It occurs in slightly younger strata than *D. sussmilchi*, and in the same area. Hence it could be expected to be a more advanced species. This is consistent with the fact that in all the characters in which the two species differ, *D. kurikae* is considered to be the more derived form. This applies not only to the remarkable specialisation of the palate and mandible for feeding but also to the reduction in 'D' bones, the increase in the size of 'X' and the division of the anterior furrow by the forward movement of the adsymphysial plate.

Speonesydrion iani occurs in the same bed at the same locality. Its 'D' bones and the anterior roofing bone pattern are more primitive, but the position of 'K' and the interrelations of the lateral lines in the 'X'–'K' area are more advanced than those of *D. kurikae*, if we accept the polarities of these characters outlined by Westoll (1949) and Miles (1977). There is no possibility of confusing these two genera in the collections. *D. kurikae* has more massive external dermal bones, a narrow snout, crudely differentiated dental apparatus and a less massive mandible, in addition to the characters listed above.

PHYLOGENETIC POSITION OF THE DIPNORHYNCHIDS

Species of *Speonesydrion* and *Dipnorhynchus* have been regarded as close relatives. Indeed *S. lehmanni* was first described as a species of *Dipnorhynchus* and was still considered as such by Miles (1977). The two genera, represented by two and three species respectively, share a number of distinctive characters — thick dentine-covered palates that increase their area by the incorporation of denticles around their free margins, dentine covering the floor of the lingual furrow and heavy tuberose heels on the prearticulars.

With the most primitive denticulate genus *Uranolophus* (see Campbell & Barwick, 1983) dipnorhynchids share the complex plating of the anterior skull roof, the meeting of the 'I' bones behind 'B', the separation of the lateral line canal in 'J'–'K'–'L' from that in 'Y_2'–'X', the fusion of the parasphenoid with the pterygoids and the large mandibular anterior furrow which is enclosed at its posterolateral extremities. Members of the denticulate group, however, have a number of distinctive features from the time of their appearance — the nature of the shedding denticles, thin palates, marginal ridges and the absence of buccohypophysial and pineal openings. Details are given by Campbell & Barwick (in press). There is no doubt that the two groups had a common ancestor which preceded them by a short interval. But it is equally clear that they had established different feeding modes that were to form the basis of two distinct lineages.

The most interesting evolutionary feature to be explored now is the relationship between the dipnorhynchids and other non-denticulate dipnoans. Given that they are the most primitive members of the 'plated' or 'dentine retaining' lineage, how are the component species related to one another and to later Devonian genera such as *Dipterus*, *Scaumenacia* and *Chirodipterus*? Of course the first of these questions points up the crux of the matter. Are the dipnorhynchids really a homogeneous group as has been commonly assumed? *Dipnorhynchus* has been regarded as the more primitive genus because its members have such crudely moulded dentitions (White, 1965; Thomson, 1967), more massive mandibles and less advanced roofing bones around 'K'. However, the matter is not as simple as that. *S. lehmanni*, from the Siegenian, is the oldest member of the group; this is suggestive but not conclusive evidence of its more primitive status. Moreover the concept of crudity of dentition as applied to these genera has no validity — the two types of dentition result from distinct developmental strategies. This type of evidence is of much greater value than roofing bone patterns since the latter are very labile even within a species, and are known to show considerable convergent and parallel evolution. Consequently the dental structures need further comparative study.

The palatal dental surfaces of species of both genera grow around their free margins only. Dentine completely covers the parasphenoid/pterygoid and pterygoid/pterygoid sutures, and consequently no bone growth can take place along these sutures without massive dentine resorption. There is no evidence that this has occurred. Additions to the lateral and posterior margins of the *Dipnorhynchus* palate took place by the growth of denticles of various sizes and their gradual incorporation into the dentine-covered surfaces by continued growth, wear and some resorption. This type of addition is well seen on the posterior and lateral parts of the palates of both *D. sussmilchi* and *D. kurikae*. The prearticular dental surfaces expanded by a similar process, and the denticles in the lingual furrow are remarkably well developed and illustrate the mechanism with great clarity.

As has been indicated above, the growth of the massive tuberosities of *Dipnorhynchus* cannot take place by the addition of large bodies of dentine at the plate margins. In the first place the dentine on them is not unusually thick, and in the second place they must migrate across the palate with growth or they would not be in a similar position on all specimens regardless of size. The only way this can be accomplished is for differential wear to occur in some areas, those that are protected by the hardest and thickest dentine gradually rising above the surrounding areas (Fig. 11). The dentine would maintain itself by pleromic growth into the underlying bone, the rate of its development in different areas being such that the tuberosities could migrate across the palate. In other words, the outline of the

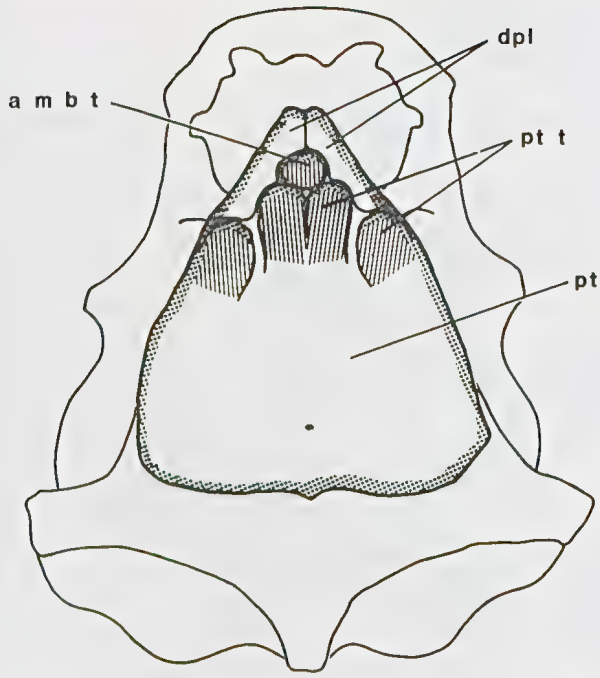

Fig. 11. Reconstruction of the palate of *D. sussmilchi*, in ventral view showing the zones of areal increase of dentine (stippled) and the zones of wear on the tuberosities (hatched). Note that as a result of this pattern, the tuberosities on the pterygoid and the anterior median bone migrate forwards and outwards, dentine growth takes place at the anterior margins of the tuberosities and the anterior and lateral margins of the pterygoids and the 'dermopalatines'. a m b t = anterior median bone tuberosity; dpl = 'dermopalatines'; pt t = pterygoid tuberosities.

palatal plates would be determined by the varying rates of marginal addition, whereas the relief on their surfaces would be determined by differential dentine growth and differential wear within the bounds of the established plate margins.

Species of *Speonesydrion* adopted a different mode of growth. Their lateral palatal margins increased by the addition of teeth which are aligned to form rows. These teeth range from simple cones to groups of denticles on the flanks of what is, in effect, an enlarged denticle (Campbell & Barwick, 1984b). Between the teeth, denticles of various shapes grew and became worn, finally coalescing at their bases to form a continuous dentine sheet crossed by radial ridges that were formed from the worn bases of old teeth. Posteriorly the plates must have expanded by the gradual incorporation of denticles in the same way as *Dipnorhynchus* plates, although the details are not so well known in the absence of good material. The prearticular plates developed radial ridges in the same way as palatal plates. The means by which they expanded is particularly well known (Campbell & Barwick, 1983, 1984b). The heel of the prearticular plate developed tuberosities by differential pleromic growth in the same way as the heel and palate of *Dipnorhynchus*.

In summary then, the plates of the two genera are similar in that they increase marginally by the incorporation of denticles, they have no bounding layer of enamel as does *Sagenodus* or *Ctenodus* and all subsequent genera, and they both produce tuberosities by similar processes. They differ in that *Speonesydrion* has differentiated the denticles on the lateral margins to produce prominent teeth which are added according to a distinctive pattern to produce plates with a small number of teeth in a small number of rows. Such plates clearly are tooth plates of the classic dipnoan type, but they are rudimentary. *Dipnorhynchus* on the other hand produces crudely sculptured plates only by differential internal growth and wear without the special modification of marginal denticles to form teeth.

Differences at this level are apparently slight, but they had profound consequences. The next member of the tooth plated line is *Dipterus*. It retained many primitive features such as a complete cosmine cover on the external dermal bones, a large number of bones on the anterior part of the skull roof and a buccohypophysial opening, but it had lost the pineal opening, separated the dentine cover on the pterygoids thus permitting growth in the mid-line, lost the dentine on the parasphenoid which in its turn had become elongated, reduced the strength of the lower jaw and produced more delicate sculpture on the tooth plates. Later members of the lineage, such as *Scaumenacia*, lost their cosmine, reduced or lost the snout ossification, decreased the number of anterior roofing bones, developed more regular radial tooth rows and laid down a continuous layer of enamel around all margins of the tooth plates. Accompanying these changes there were considerable modifications to the histology of the tooth plates. These have been outlined by Smith, Smithson & Campbell (in prep.).

The genera that developed tuberosities rather than teeth, and thus produced dentine plates rather than tooth plates in the terminology of Smith & Campbell (in prep.), followed somewhat different evolutionary lines. The next members of this lineage after *Dipnorhynchus* are *Stomiahykus*, from the Eifelian and *Chirodipterus* from the Frasnian. In these genera the marginal denticles were modified into elongate blisters which added bodies of dentine to the margins of the plates, and they began to develop radially arranged tuberosities composed of hard pleromic dentine. It is interesting that *Stomiahykus* retains 'dermopalatines' fused to the pterygoids, pterygoid plates meeting in the mid-line, a parasphenoid fused to the pterygoids, and dentine on the parasphenoids, whereas *Chirodipterus* has free 'dermopalatines' that do not meet medially, separated pterygoids and parasphenoid, and no dentine on the parasphenoid. In addition the plates of *Chirodipterus* have developed petrodentine (Smith, 1984). Like the roofing bone changes referred to above, these changes parallel those of the tooth-plated genera.

If *Speonesydrion* is the first known member of a lineage leading to tooth-plated types and *Dipnorhynchus* is in a comparable position in relation to dentine-plated types, the Dipnorhynchidae would be a grade group or, in cladistic terms, a paraphyletic group.

If Smith and Campbell are correct in separating tooth-plated and dentine-plated types into distinct lineages, and it seems impossible to convert one type into the other, the amount of parallelism within these lineages like that between the denticulated lineage and the plated lineages together, is very considerable. Once again attempts to infer relationships by seeking to minimise parallelisms and convergences on the grounds that such a procedure satisfies the requirements of parsimonious argument, is called into question. The nature of the genetic code should have alerted us to the point that parallelism and convergence could be expected to be a widespread rather than an exceptional result of the evolutionary process. This is now being exemplified by such work as that of Sibley and Ahlquist (1985) on Australian passerine birds. What is needed for the elaboration of the palaeontological data is more sophisticated analysis of comparative morphology and less speculation based on philosophical presuppositions about the nature of the evolutionary process.

THE PRIMITIVE DIPNOAN PLATE

The morphotype from which tooth plates and dentine plates were derived can now be reconstructed. We hypothesise that it had the following characteristics: (a) continuous dentine across the pterygoids and the lingual furrow, precluding the addition of dentine in the mid-line in either jaw; (b) addition of dentine at the lateral and posterior margins of the pterygoids and prearticulars by the incorporation of denticles of uniform size; (c) lack of differential pleromic growth on the plates except perhaps for the heel of the prearticulars; (d) absence of radial ridges or any other eminences on the plate surfaces, as the result of the above growth patterns; and (e) thin dentine with irregular pulp canals growing directly on the basal bone and with a minimum of bone resorption to permit downward dentine growth.

Note that this hypothesis requires the presence of denticles around the plate margins. These denticles were attached to the basal bone and were gradually incorporated into the continuous dentine sheet. They were not of the shedding type which characterised the denticulate lineage of Campbell & Barwick (1983). Dealing with a similar case of confusion resulting from a failure to recognise comparable entities of different origins Read (1948) noted that there are 'granites and granites'. We reiterate that in our view there are 'denticles and denticles'.

So far as can be determined at present, the Dipnoi differentiated from other bony fishes by the development of a palatal bite. Associated changes were the holostylic jaw suspension, the development of distinctive muscle chambers in the cranium and unique cristae to brace the roof to the braincase, the evolution of the broad mandible with larger open rami for the insertion of the adductor muscles and the covering of the palate and the 'prearticulars' with hard-wearing dentine. As we have shown elsewhere, it is not possible to homologise the bones of the palate with those of tetrapods (Campbell & Barwick, 1984a), and it has long been known that there are major difficulties in accounting for the absence of such bones as the coronoids in the mandible. Despite attempts to show that premaxillae and maxillae are present as modified tooth bearing bones in early dipnoans, supporting arguments have been shown to be dubious (Campbell & Barwick, 1984b). Skull roof differences are also manifest. The Dipnoi is the only group which primitively has five longitudinal rows of bones across the posterior part of the roof (Schultze & Campbell, in press), and the arrangement of the lateral line canals on the skull and mandible is distinctive (Gardiner, 1984).

The time has come to consider seriously the argument, based on the excellent fossil material now available, that this type of organism with its palatal bite became separated from other bony fishes before the premaxillae, maxillae, distinctive roofing bone patterns, pterygoids, 'dermopalatines', dentaries, prearticulars and coronoids differentiated from the matrix of small dermal bones in ancestral osteichthyans. Such an analysis is now feasible and could be undertaken to counter the views on the phylogenetic relationships of the Dipnoi derived from comparison of the highly derived characters of the extant genera of the group (Rosen *et al.*, 1981).

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Cardomanica andersoni n.gen., n.sp. from the Western Tasman Sea with Notes on Species from the Tropical Western Atlantic Ocean (Crustacea: Ascothoracida: Synogogidae)

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Abstract. *Cardomanica andersoni* n.gen., n.sp. is described from the western Tasman Sea where it lives on the gorgonacean *Chrysogorgia orientalis* Versluys. This is the first record of a synagogid ascothoracidan from the South Pacific Ocean. The recently described synogogid, *Isidascus longispinatus* Grygier from the western Atlantic Ocean, is transferred to *Cardomanica* and split into two species, *C. longispinata* (Grygier) and *C. quadricornuta* n.sp.

Lowry, J.K., 1985. *Cardomanica andersoni* n.gen., n.sp. from the western Tasman Sea with notes on species from the tropical western Atlantic Ocean (Crustacea: Ascothoracida: Synogogidae). Records of the Australian Museum 37(6): 317–323.

Keywords: Ascothoracida, Synagogidae, *Cardomanica*, Tasman Sea, Atlantic Ocean, taxonomy.

During a recent ground fish survey off south-eastern Australia Mr Ken Graham (Division of Fisheries, New South Wales Department of Agriculture) collected sediment and benthic invertebrates from demersal trawls. From this collection, Mr Phil Colman (Malacology, Australian Museum) sorted an interesting bivalved animal which he recognized as a crustacean. These ascothoracidan specimens were living in an inverted orientation on the branches of the small, bushy gorgonacean, *Chrysogorgia orientalis* Versluys. They are described below as a new genus and species, *Cardomanica andersoni*, in the ascothoracidan family Synagogidae. Grygier (1984) recently described *Isidascus longispinatus* from the tropical western Atlantic Ocean. Based on his detailed description I am transferring *I. longispinatus* to *Cardomanica* and splitting his material into two species, *C. longispinata* and *C. quadricornuta* n.sp.

Cardomanica n.gen.

Diagnosis. Based on female. Carapace completely enclosing body, forming a large dorsal brood chamber; ventral margins rounded, opening to the outside through a slit; anterior margin produced into a sleeve-hinge which is sealed from the body by a partition, and which overlaps a branch of the gorgonacean host to form a permanent attachment. Antennules large, obviously 6-articulate and prehensile; article 3 oblong; article 4 with 2 setae; article 5 as long as article 6; article 6 with 2 posterodistal processes close together behind sharp falcate claw. Oral cone bellows-like with styliform tip; mandibles and maxillules complexly armed, maxillae smooth with bifid tip, but no hook, medial languette present. Thoracic segments 2 to 4 or 5 each with a dorsomedial 'horn'. Thoracopods biramous. First thoracopod with 2-articulate exopod and endopod; coxa with lateral seta and with long attenuated filamentary appendage at base. Thoracopods 2 to 5 with 2-articulate exopod and 3-articulate endopod; coxa 2 to 4 with lateral seta. Sixth thoracomere bearing large epaulet; thoracopod small; coxa without lateral seta. Abdomen 5-segmented; first segment with large slender biramous penis; fifth segment with 2 large telsonic spines; furcal rami tapered, blunt and downturned, each with some terminal setae, no ventral setae and many medial setae.

Type-species. *Cardomanica andersoni* n.sp.

Etymology. The generic name is derived from the Latin words 'cardo' (sleeve) 'manica' (hinge) and alludes to the attachment mechanism of the ascothoracidan to its gorgonacean host.

Remarks. *Cardomanica* is most closely related to *Gorgonolaureus* Utinomi, 1962 (redefined, Grygier, 1981), *Isidascus* Moyse, 1983 and *Thalassomembracis* Grygier, 1984. All of these genera have a fused bivalve carapace which completely encloses the body, forming a large dorsal brood chamber in the female, and with a ventral aperture to the outside. In *Cardomanica*, *Gorgonolaureus* and *Isidascus* there is a large dorsomedial 'horn' on at least the second thoracomere. The styliform mouthparts in all three genera are very

similar, as is the setation on the antennules.

Cardomanica differs from all other synagogids in the method of host attachment. Species of *Cardomanica* have a neat sleeve-hinge which clamps around the branches of the gorgonacean host. Species of the other three genera are also attached to the axes of the host by means of the carapace, but in different ways. Probably all species in these genera are covered by host tissue.

Cardomanica differs from *Gorgonolaureus* in having a large ventral aperture on the carapace, multiple rows of setae on the maxillules, no posterior hooks on the maxillae, basal teeth on the mandible, both posterior processes on article 6 of the antennule located distally just behind the claw, a filamentary appendage at the base of coxa 1, tapering furcal rami and well developed telsonic spines.

Cardomanica differs from *Isidascus* in having posterior setae on article 2 of the antennules, basal teeth on the mandibles, bifid maxillary tips, no laterodistal coxal setae on the fifth thoracopod, a biramous penis in adult females, and tapering furcal rami.

Cardomanica differs from *Thalassomembracis* in not having grapnels or a single anteroventral anchor on the carapace, in not having posterior hooks on the maxillae and in having a well developed biramous penis.

Cardomanica andersoni n.sp.

Figs 1–3

Type-material. HOLOTYPE, female (brooding 195 nauplii), carapace 6.4 mm long and 6.5 mm high, body 4.5 mm long, Australian Museum AM P34357; PARATYPE, carapace 7 mm long and 7 mm high, body 4.4 mm long, AM P34356; 8 PARATYPES, at least 2 of which are brooding females AM P34358; off Ulladulla, New South Wales, Australia, 35°39′S 150°52′E, living on the gorgonacean *Chrysogorgia orientalis* Versluys in 950 m depth, K.J. Graham on FRV *Kapala*, 8 September 1983, station K83-11-04.

Additional material. 7 specimens, AM P34359, off Ulladulla, New South Wales, Australia, 35°29′S 150°53′E, living on the gorgonacean, *Chrysogorgia orientalis* in 1000 m depth, K.J. Graham on FRV *Kapala*, 25 October 1983, K83-14-02; 2 specimens, AM P34360, off Shoalhaven Bight, New South Wales, Australia, 34°52′S 151°14′E, living on *C. orientalis* in 1000 m depth, K.J. Graham on FRV *Kapala*, 26 October 1983, K83-14-04; 1 specimen, AM P34361, off Shoalhaven Bight, New South Wales, Australia, 34°53′S 151°14′E, living on *C. orientalis* in 1050 m depth, K.J. Graham on FRV *Kapala*, 26 October 1983, K83-14-05; 2 specimens, AM P34362, off Broken Bay, New South Wales, Australia, 33°37′S 152°06′E, living on *C. orientalis* in 990 m depth, K.J. Graham on FRV *Kapala*, K83-14-08.

Diagnosis. Carapace not papillate, 6.4 mm long x 6.5 mm high (ratio 1:1), ventral margin rounded. Thoracomeres 2 and 3 each with a long, slender, asetose dorsomedial 'horn', thoracomere 4 with a short, asetose dorsomedial 'horn'. Thoracopods 1 to 6 on one side of body with about 250 setae altogether, terminal articles of endopods with about 57 setae, terminal articles of exopods with about 84 setae (Table 1).

Description. Carapace (Fig. 1A–D) 6.1 mm long and 6.8 mm high, formed of 2 partially fused valves completely enclosing body; anterodorsal margins oblique, dorsal and posterodorsal margins evenly rounded, dorsal margins fused to form a large brood chamber in female; ventral margins evenly rounded, not fused, forming a slit. Anterior margins produced into overlapping sleeve-hinge; lower inner margin of sleeve-hinge bearing short cuticular teeth. Internal structure of the cuticle of the carapace gives the false impression of surface papillae under the light microscope.

Body (Fig. 1F–E) attached to carapace by adductor muscles within head. Head fits against anterior partition which separates main body from sleeve-hinge. Antennules attached anteroventrally with antennae immediately adjacent; styliform mouthparts attached ventrally. Thoracic region 6-segmented, first thoracomere completely free from head with fringe of hairs along anterior margin and thoracopods set off from others. Second and third thoracomeres with long dorsomedial 'horns' over 1.5 times as long as thoracomere height. Fourth thoracomere with a short dorsomedial 'horn'. Abdomen 5-segmented with first segment bearing elongate bifurcate penis and sixth segment bearing 2 large, recurved telsonic spines and 2 furcal rami.

Antennules (Fig. 2A) 6-articulate, prehensile, article 6 closing onto article 5; article 2 with a clump of setae along posterior margin; article 3 broader than long with anterior margin about twice as long as posterior margin, surface covered in groups of minute comb setae, anterior margin densely covered with setae; article 4 broader than long, surface covered in minute comb setae, anterior margin with two setae; article 5 about 1.75 times as long as broad, tapering distally and bearing about 10 stout setae along anterior margin; article 6

Table 1. Thoracopodal setal count for holotype of *Cardomanica andersoni*. Positions 1–9 are identified in Figure 3F. Parentheses indicate fused articles in the endopods of thoracopods 1 and 6.

	Position on limb								
Thoracopod	1	2	3	4	5	6	7	8	9
T1	1	0	0	18	15	(1)		0	0
T2	1	0	0	14	8	3	4	13	10
T3	1	0	1	13	8	3	4	12	12
T4	1	0	1	15	8	3	4	12	10
T5	0	0	1	13	9	2	2	4	0
T6	0	0	0	11	9	(1)		2	0

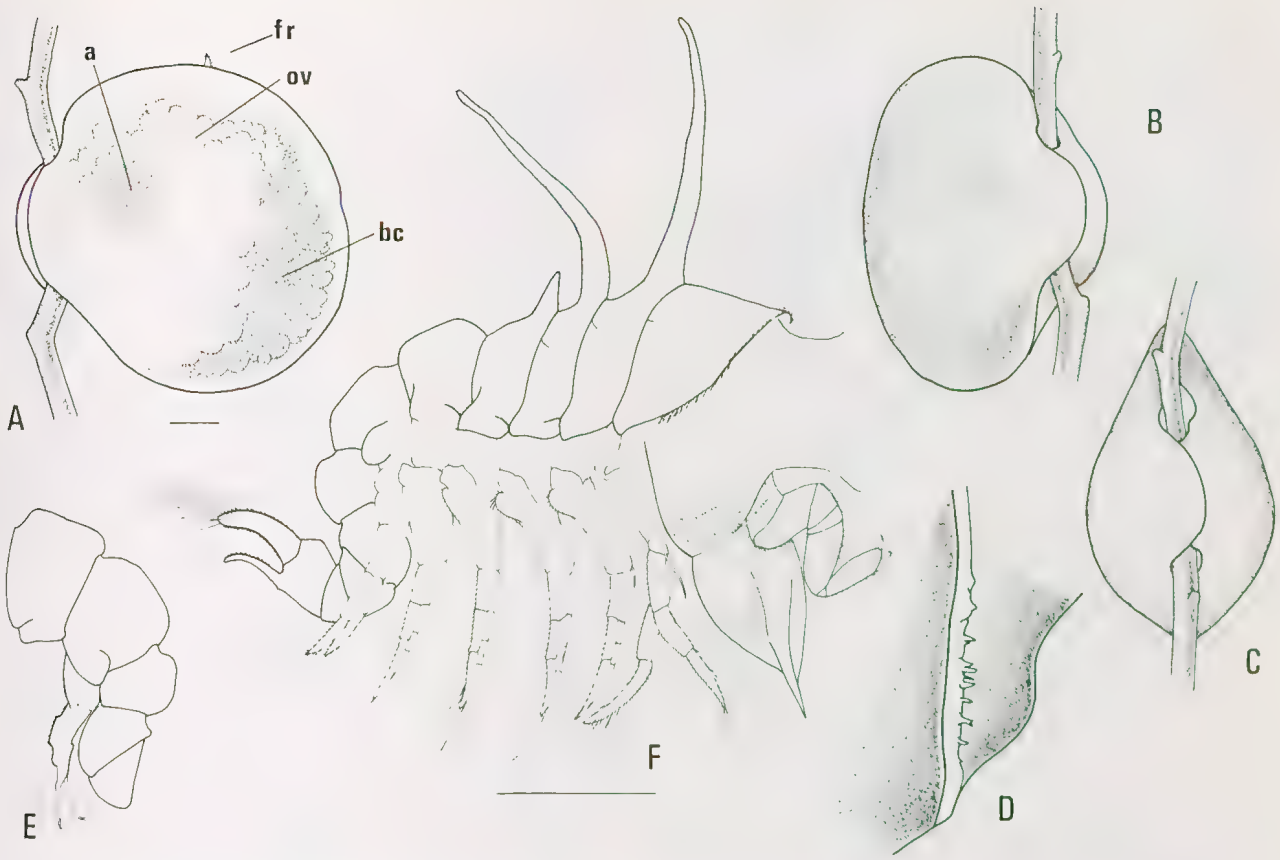

Fig. 1 *Cardomanica andersoni* n.gen., n.sp., holotype female AM P34357. Off Ulladulla, NSW, Australia, 950 m depth. **A**, lateral view of carapace attached to gorgonacean host *Chrysogorgia orientalis* Versluys. **B**, foreshortened lateral view showing sleeve-hinge attachment to host. **C**, anterior view of sleeve-hinge attachment to host. **D**, inner margin of sleeve-hinge partition showing cuticular teeth. **E**, left side of abdomen showing penial process. **F**, right side of whole animal extracted from carapace. a, adductor muscle; bc, brood chamber; fr, furcal ramus; ov, ovaries. Scales represent 1 mm.

more than 3 times as long as broad and subequal in length to article 5, posterior margin with several rows of comb setae, process just proximal to claw guard on posterodistal margin bears a basally arising aesthetasc and 3 terminal setae, claw guard broad, concave with 3 large and 1 small terminal setae and an articulating tip covered in short hairs; claw smooth, sickle-shaped. Antenna (Fig. 2B) small, not well developed, not articulate and bearing a number of small distal setae.

Oral cone bellows-like; mouthparts, surrounded by labrum, long and styliform together forming a piercing and sucking mechanism. Mandibles (Fig. 2C) broad basally and tapering to a stylet tip, inner margin bearing a row of many curved teeth which become setose distally, curved outer margin with short setae distally and sparse long hairs proximally. Maxillule (Fig. 2E) similar in shape to mandible but stronger, tip forming a concave inner surface with stiff hairs along the raised margins and softer hairs medially. Maxillae (Fig. 2F) fused proximally, bearing thin lateral flanges distally, and terminating in a bifurcate tip. Medial languette (Fig. 2D) triangular, bearing numerous minute hairs near medial margin.

Thoracopod 2 (Fig. 3B) with 3 seminal receptacles, thoracopods 3 to 5 (Fig. 3A) each with 6 seminal receptacles in coxae. Thoracopod 1 (Fig. 3E) separated from others, protopod slender; coxa with distolateral seta; inner surface of basis covered in long hairs; exopod 2-articulate, covered in long hairs, second article with about 8 stout setae covering inner surface and 3 long terminal plumose setae; endopod 2-articulate, covered in long hairs with several surface setae, 4 terminal plumose setae and 8 plumose setae along outer margin on article 2, article 1 with 1 distolateral plumose seta. Thoracopods 2–5 (Fig. 3F) similar, 2-articulate exopod and 3-articulate endopod; coxa broad with distolateral seta except in thoracopod 5, long hairs along lateral margin, and comb setae and long plumose setae along medial margin; exopod slightly longer than endopod with long hairs along lateral margins and plumose setae along inner margins of article 2 of exopod and all 3 articles of endopod. Thoracopod 6 (Fig. 3C) smaller than the rest; protopod narrow, fused with some hairs along inner margin; exopod longer than endopod, articles nearly fused, with long marginal hairs, 4 long plumose setae terminally and 3 to 4 long plumose setae distomedially; endopod, articles nearly fused with rows of comb setae along surface, 2 long plumose setae terminally and 5 along margin.

Abdomen (Fig. 1E, F) 5-segmented; segment 1 with

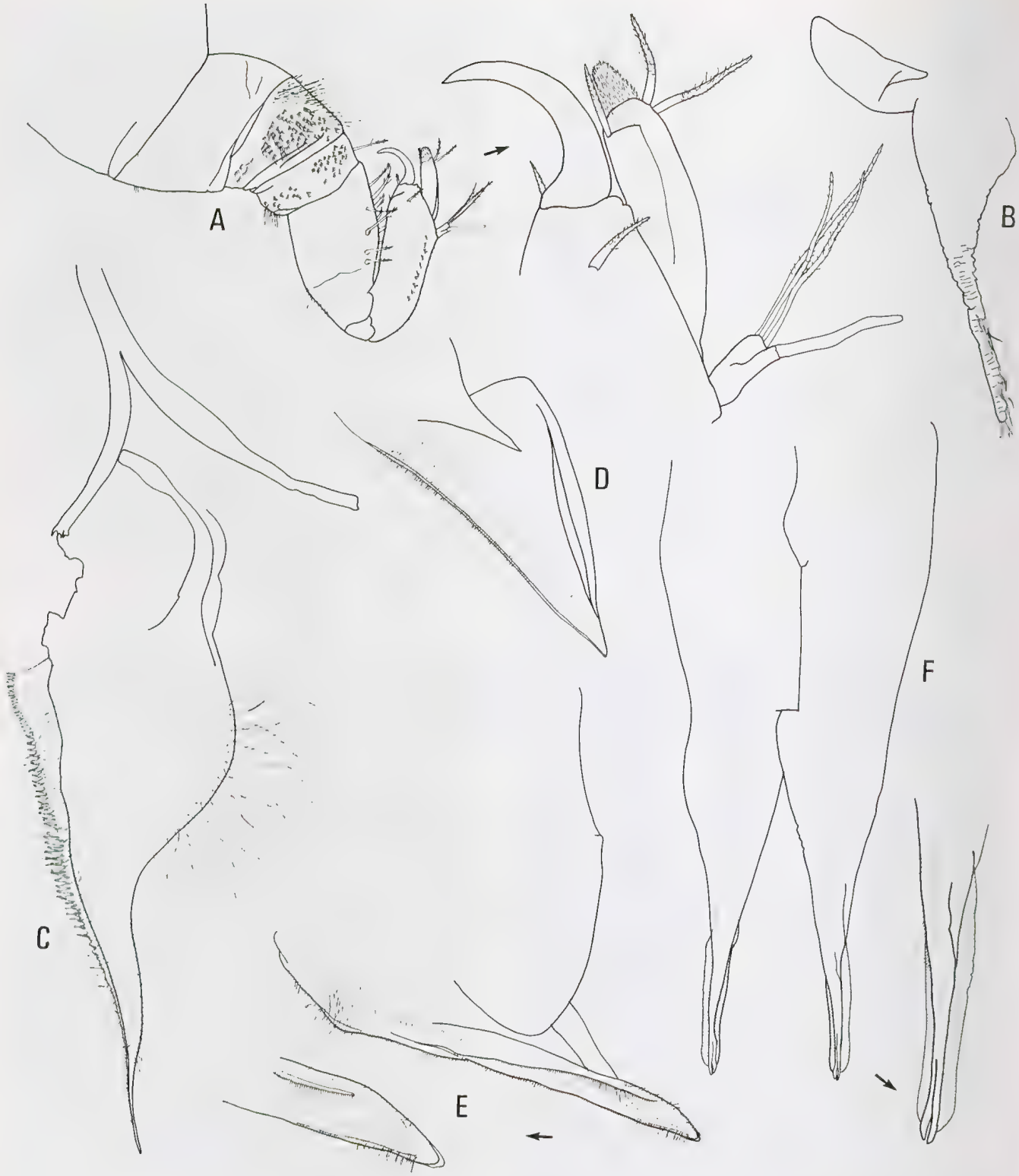

Fig. 2. *Cardomanica andersoni* n.gen., n.sp., paratype AM P34356. Off Ulladulla, NSW, Australia, 950 m depth. **A**, antennule with detail of tip. **B**, antenna. **C**, mandible. **D**, medial languette. **E**, maxillule with detail of tip. **F**, maxilla with detail of tip.

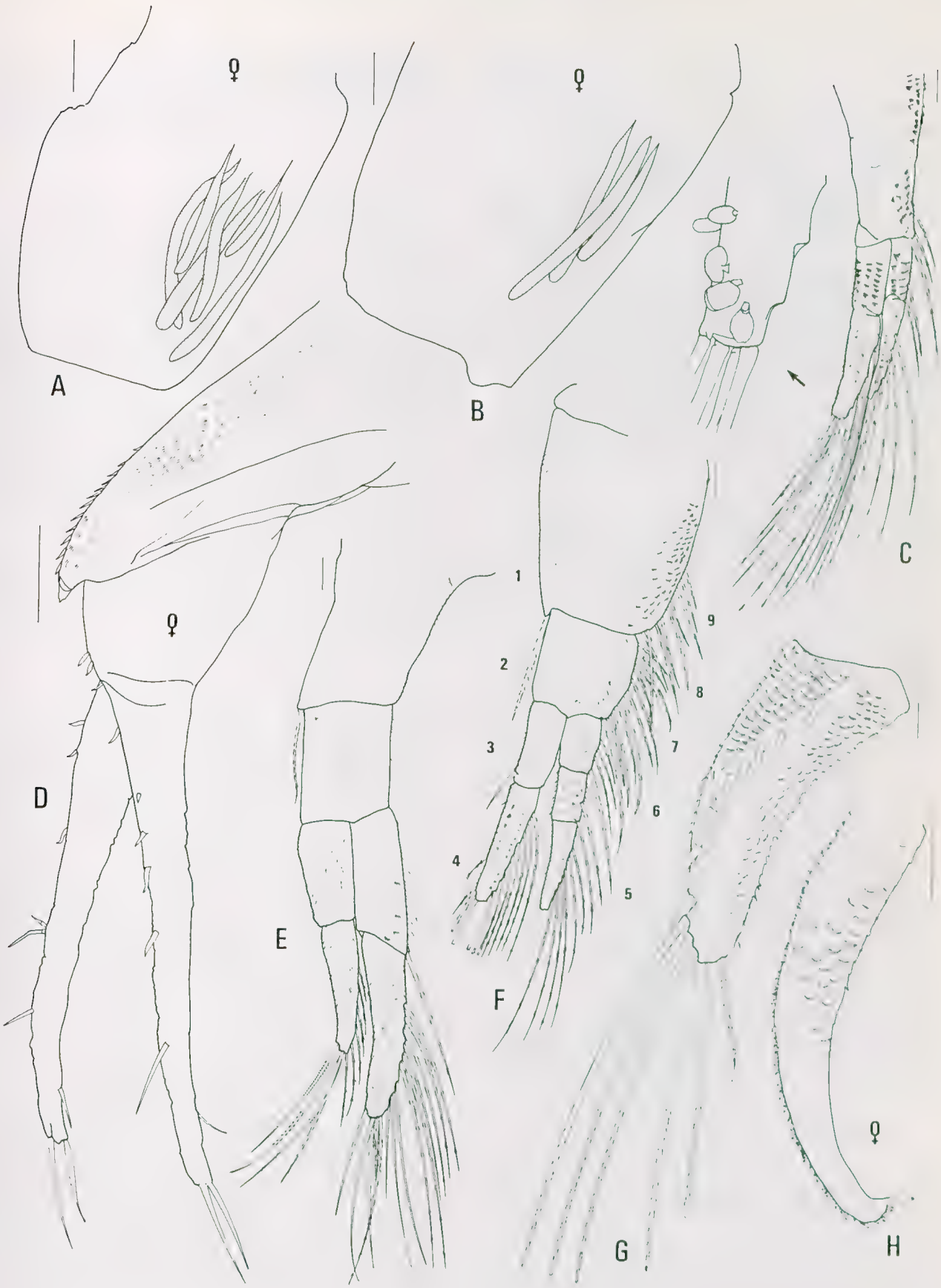

Fig. 3. *Cardomanica andersoni* n.gen., n.sp., holotype AM P34357 and paratype AM P34356. Off Ulladulla, NSW, Australia. **A**, coxa of thoracopod 4 containing 6 seminal receptacles. **B**, coxa of thoracopod 2 containing 3 seminal receptacles. **C**, thoracopod 6, enlargement of distal end of endopod showing chonotrich commensals. **D**, penial process. **E**, thoracopod 1. **F**, thoracopod 2. **G**, furcal ramus. **H**, telsonic spine.

Table 2. Characters differentiating species of *Cardomanica*.

	Carapace	Thoracomere 'horns'	Thoracopods 1 to 6, sete on terminal articles	
			endopods	exopods
C. andersoni	not papillate	2 to 4, naked	57	84
C. longispinata	not papillate	2 to 4, setose	42	74
C. quadricornuta	papillate	2 to 5, setose	62	86

well developed biramous penis; segment 5 with 2 large telsonic spines (Fig. 3H), subequal in length to furcal rami but narrower, recurved distally and bearing minute denticles along dorsal margin; furcal rami (Fig. 3G) recurved distally with ventral and dorsal margins serrate, and comb setae over much of surface, 1 short and 2 long terminal plumose setae and 15 medial plumose setae.

Etymology. This species is named for Professor D.T. Anderson in recognition of his contribution to the biology of Crustacea.

Remarks. The three known species of *Cardomanica* appear to be closely related (Table 2). The antennules, mouthparts, thoracopods, furcal rami and telsonic spines are almost identical between the species. *Cardomanica andersoni* and *C. longispinata* both have two long and one short dorsomedial 'horns', but in *C. andersoni* the two long 'horns' are much longer, more slender and without setae. The thoracopods of *C. andersoni* are more setose than those of *C. longispinata*, particularly the terminal articles of the endopods and exopods. The length to height ratios of the carapaces in both species are also similar (about 1 x 1), but the carapace of *C. andersoni* has a more rounded ventral margin and is about 1.5 times as large as the carapace of *C. longispinata*.

Cardomanica andersoni and *C. quadricornuta* are very similar in the number and arrangement of thoracopodal setae. The carapace of each species is of similar size although the length to height ratios differ, 1 x 1 in *C. andersoni* and 1 x 1.3 in *C. quadricornuta*. But *C. quadricornuta* differs in having a papillate carapace and four setose dorsomedial 'horns' on thoracopods 2 to 5.

Cardomanica andersoni is currently known only from the deep continental slope (about 1000 m) of the western Tasman Sea off New South Wales. It lives attached to the gorgonacean, *Chrysogorgia orientalis* Versluys.

Cardomanica longispinata (Grygier, 1984) new combination

Isidascus longispinatus Grygier, 1984: 143 (in part, figs 1A–C, E, G–I and 2A–I, M, O–Q, table 1), remainder = *C. quadricornuta*.

Diagnosis. Carapace not papillate, 4.6 mm long x 4.3 mm high (ratio 1.1:1), ventral margin straight. Thoracomeres 2 to 4 each with a short, thick, setose dorsomedial 'horn' becoming progressively shorter posteriorly. Thoracopods 1 to 6 on one side of body with about 200 setae altogether, terminal articles of endopods with 42 setae, terminal articles of exopods with 74 setae (Grygier, 1984, table 1).

Remarks. *Cardomanica longispinata* was originally placed in *Isidascus* Moyse, 1983. But *C. longispinata* is excluded from *Isidascus* in the ways outlined earlier. *Cardomanica longispinata* differs from *C. andersoni* in the ways discussed under that species (Table 2). It differs from *C. quadricornuta* in having a smaller, non-papillate carapace with a different length to height ratio, only three dorsomedial 'horns', and fewer setae on the thoracopods, particularly the terminal articles of the endopods and exopods.

Cardomanica longispinata is currently known from off Colombia and in the Gulf of Mexico, western Atlantic Ocean living on *Chrysogorgia elegans* Verrill and another undetermined species of *Chrysogorgia* in depths of 366 to 567 m.

Cardomanica quadricornuta n.sp.

Isidascus longispinatus Grygier, 1984: 143 (in part, figs 1D, F and 2J–L, N, table 1), remainder = *C. longispinata*.

Type-material. HOLOTYPE female USNM 191231 on *Chrysogorgia* cf. *elegans* USNM 344508; north of Bahamas, 26°06′N 77°08′W, 1023–1153 m, R. Carney on RV *Columbus Iselen*, 21 October 1980, Cr. 8007, stn 063.

Diagnosis. Carapace papillate, 6.7 mm long x 8.7 mm high (ratio 1:1.3), ventral margin straight. Thoracomeres 2 to 5 each with a setose dorsomedial 'horn' becoming progressively shorter posteriorly. Thoracopods 1 to 6 on one side of body with about 250 setae altogether, terminal articles of endopods with 62 setae, terminal articles of exopods with 86 setae (Grygier, 1984, table 1).

Etymology. This species is named for the four dorsomedial 'horns' on thoracomeres 2 to 5.

Remarks. In the original description of *C. longispinata* Grygier (1984) described differences between his material from Colombia and the Gulf of Mexico and his material from north of the Bahamas. At the time he did not think the evidence warranted establishing separate species. But with the discovery of another, closely related species in the Tasman Sea the differences between the Colombia/Gulf of Mexico material and the Bahaman material become significant. The Bahaman material must be considered a separate species which differs from other species of *Cardomanica* in the ways discussed earlier (Table 2).

Cardomanica quadricornuta is currently known from

only one specimen collected on *Chrysogorgia* cf. *elegans* Verrill north of the Bahamas, western Atlantic Ocean, in about 1000 m depth.

ACKNOWLEDGEMENTS. I thank Mr Ken Graham, Division of Fisheries, New South Wales Department of Agriculture, for collecting *Cardomanica andersoni*, Mr Phil Colman, Autralian Museum, for bringing them to my attention and Mr Phil Alderslade, Northern Territory Museum, Darwin, for identifying the gorgonacean host. I also thank Ms Sharne Dunlop for the whole animal illustrations and Mr Roger Springthorpe, Australian Museum, for composing and inking the plates. Finally, I thank Dr Mark Grygier, Scripps Institution of Oceanography, for critically reading and making many useful comments on the manuscript.

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Siphonoecetinae (Crustacea: Amphipoda: Corophiidae) 4: *Australoecetes* Just, 1983, including *Stebbingoecetes* n. subgen.

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ABSTRACT. Based on type material and old unpublished collections as well as recently collected material *Australoecetes* Just, 1983 is fully described. *A. sellicki* (Sheard, 1936) and *A. australis* (Stebbing, 1910) are redescribed and lectotypes selected. *Australoecetes jervisi* n. sp. is described. Based on morphological and correlated biological differences two subgenera are recognized: *Australoecetes* (with *A. sellicki*, east to west southern Australia) and *Stebbingoecetes* n. subgen. (with *A. australis*, type-species, and *A. jervisi*; both from south-eastern Australia).

JUST, J., 1985. Siphonoecetinae (Crustacea: Amphipoda: Corophiidae) 4: *Australoecetes* Just, 1983, including *Stebbingoecetes* n. subgen. Records of the Australian Museum 37(6): 325–341.

KEYWORDS: Amphipoda, Corophiidae, Siphonoecetinae, *Australoecetes*, Australia, taxonomy, biology.

The first siphonoecetine described from Australia was *Siphonoecetes australis* Stebbing, 1910. Sheard (1936) described a second species, *S. sellicki*, from the Gulf of St Vincent, South Australia. Ruffo (1959) placed *S. sellicki* in synonymy of *S. australis*. Just (1983) erected a new genus, *Australoecetes*, establishing *S. sellicki* Sheard, 1936 as type-species and including *S. australis* Stebbing, 1910. The reason for selecting *S. sellicki* for type-species was the homogeneity of the syntype material; the extant syntype material of *S. australis*, on the other hand, consists of two specimens, one of which belongs in an undescribed genus and species.

During my recent field work in Australia (1984), and sorting through old and new collections primarily in the Australian Museum and the Museum of Victoria, material of the two historical species was found. In addition, an undescribed species closely related to *A. australis* was collected in Jervis Bay, New South Wales.

Biologically *A. australis* and *A. jervisi* n.sp. conform with the normal siphonoecetine way of occupying empty mollusc shells or other suitable abodes (e.g. polychaete tubes), in which they crawl around on top of the sediment. *Australoecetes sellicki*, however, is unique in that it selects for abodes very light materials (normally hollow stem nodes from *Amphibolis* sea grass, occasionally other materials). This enables the specimens to swim away from the bottom with their house by aid of the unique long natatory setae on the peduncle of antenna 2.

The present study has shown that, although the three species differ from all other siphonoecetines as outlined in the original diagnosis of *Australoecetes*, they fall into two distinct groups (*A. sellicki*, and *A. australis* plus *A. jervisi* n. sp.). The main differences are found in the antennal armature, including the presence in *A. sellicki* of true spines on flagellar articles of antenna 1 and of natatory setae in antenna 2.

Differences between the two groups in mouthparts (e.g. mandibular palp, notched *versus* entire upper lip), in coxal plates and in details of the uropods, may be of taxonomic significance at the generic level, but more information on the intrageneric stability of such characters from other goups of siphonoecetines is needed.

The two groups are here considered as subgenera of *Australoecetes*. Distribution of the three species is shown in Fig. 1.

Scales and signatures referring to Figs 3–13 are given in Fig. 2. The term mature female refers to a female with fully developed oostegites (ovigerous, with embryos or with an empty marsupium).

A list of institutional and descriptive abbreviations follows:

AM	Australian Museum, Sydney
NMV	Museum of Victoria, Division of Natural History, Melbourne.
SAM	South Australian Museum, Adelaide
ZMUC	Zoological Museum, University of Copenhagen
a	antenna
ar	article

c	cephalon
cx	coxal plate
dv	dorsal view
f	flagellum
ll	lower lip
lv	lateral view
md	mandible
mp	maxilliped
mv	medial view
mx	maxilla
p	pereopod
pa	palp
pl	pleopod
pls	pleonal sideplate
r	right
s	seta
u	uropod
ul	upper lip
us	urosome
vp	ventral projection, article 2 of antenna 2
vv	ventral view

Unless otherwise stated left side appendages have been used for illustrations. Length of animals has been measured from tip of rostrum along dorsal curvature to apex of telson.

Fig. 1. Distribution of species in *Australoecetes* s.l.

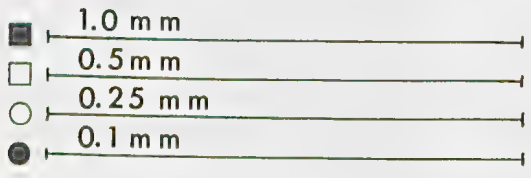

Fig. 2. Scales referring, by signature, to details in Figs 3–13.

Australoecetes Just, 1983

Remarks on diagnosis. The diagnosis of *Australoecetes* stated (Just 1983: 128) that the inner ramus of uropods 1 and 2 are at most half as long as the outer ramus. This is not correct for uropod 2, in which the inner ramus may be up to ¾ the length of the outer ramus.

Description. Cephalon and body with a few scattered monoflagellate obliquely inserted setules. Rostrum in lateral view absent or tiny, anterior cephalic margin forming a pointed angle of ca. 90° in dorsal view. Subrostral projection pointed, laterally compressed, reaching ¼ to ⅓ the length of peduncular article 1 of antenna 1. Eye lobes rounded in dorsal view, bluntly produced in lateral view, ocellar area inflated.

Mouthparts normal siphonoecetine (Just 1983). Upper lip broader than long, apically notched or entire. Mandibular palp with tiny article 2 inserted centrally in apex of article 1. Maxilla 1: palp slender with nearly parallel margins, reaching well beyond apical spines of outer plate, apex oblique with slender spines and a few subapical setae; inner plate without setae. Maxilla 2: plates of subequal length with rounded apex, outer plate broader than inner plate. Maxillipeds: outer plate reaching apex of article 2 of palp, with 1 apical pectinate seta followed medially by up to 14 strong spines.

Antenna 1 reaching ½ to ⅔ along peduncular article 5 of antenna 2; flagellum with 3–6 articles, about as long as peduncular article 2. Antenna 2: ventral projection of peduncular article 2 with rounded apex carrying apical and distolateral setae; articles 4 and 5 of subequal length; flagellum 50–70% the length of peduncular article 5, with 2 ventral spines apically on article 3 and 1 apical ventromedial spine on article 2.

Coxal plates 1–2 or 1–3 slightly overlapping, others discontinuous; all plates with sparse marginal setation.

Pereopod 1 simple, dactylus with posterior denticles; article 6 with posterior apical tooth and 2–3 midposterior spines, medial surface with short transverse rows of long pectinate setae, article 6 subequal to or up to 20% longer than 5; article 5 without spine on posterior lobe. Pereopod 2 simple, oval, broader than 1, dactylus with posterior denticles, article 6 with posterior apical tooth, 1 large midposterior spine and 2–4 smaller proximal spines; article 6 subequal to or up to 20% longer than 5; article 5 without spine on posterior lobe. Pereopods 3–4: article 4 with anterior and posterior lobes equally well developed, both reaching apex of or slightly overreaching article 5; article 5 without posterior spines. Pereopod 5–6: article 5 with 1 slender curved spine apically and one to several short subapical-lateral spines.

Pleopods with medially expanded peduncle of subrectangular shape, carrying two coupling hooks; rami broad with incomplete articulations, inner ramus about as long as width of peduncle, outer ramus ¾ to ⅘ the length of inner ramus.

Uropods 1–2: ventral apical margin of peduncle with broadly rounded expansion covering part of rami; outer

ramus normal, slightly curved; inner ramus shortened, plate like, somewhat spoon shaped with concave surface facing outer ramus, distal margin with sharp denticles, apex with at most 1 short spine. Uropod 3; peduncle with strongly tapering mediodistal expansion carrying 2–4 mediodistal setae; ramus about as long as broad or slightly longer, apex rounded with 3–5 long pectinate setae, ventral articulation with peduncle distinct, dorsal articulations often very indistinct.

Telson broader than long, of rounded to subrectangular shape, with small oval spine fields in distolateral corners, and midlateral groups of 3–4 small setae (often 3 plumose and 1 simple).

Oostegites with setae in distal half, setae with microdenticulate apex and subapical micropectination.

Type-species. *Siphonoecetes sellicki* Sheard, 1936 (original designation).

Component species. *Australoecetes australis* (Stebbing, 1910), *A. jervisi* n.sp., *A. sellicki* (Sheard, 1936).

Subgenus *Australoecetes*

Diagnosis. *Australoecetes* with ventroapical spine on some or all flagellar articles of antenna 1. Peduncular articles 4 and 5 of antenna 2 with lateral and in particular medial transverse rows of long, plumose, curved, forward pointing setae (natatory). Inner ramus of uropods 1 and 2 without apical spine.

Description. The following characters also separate *Australoecetes* s.s. from the new subgenus described below: cephalon markedly flattened, ca. 1½ times longer than deep. Upper lip with entire, setulose apex. Mandibular palp short, slender, subcylindrical. Coxal plate 1 broader than anterior length, rectangular. Pleopods with peduncle as broad as long. Uropods 1 and 2, outer ramus with 3 and 1 short apical spines respectively, inner ramus with broadly rounded denticulate apical margin.

Type-species. *Siphonoecetes sellicki* Sheard, 1936.

Component species. Type-species, as *Australoecetes sellicki* (Sheard, 1936).

Australoecetes sellicki (Sheard, 1936)
Figs 3–7

Siphonoecetes sellicki Sheard, 1936: 450, fig.2.
Australoecetes sellicki n.comb. — Just, 1983: 128.

Notes on type-material. Sheard (1936) based his description on eight specimens "... collected in January 1936, by Mr. H.M. Hale... in a small rock pool at Sellicks Reef, ...", together with one specimen collected at a later date, "... Types in the South Australian Museum, Reg. No. C 2114, C 2117".

The South Australian Museum has a sample marked C2114 containing six specimens of *Siphonoecetes sellicki* Sheard (marked paratypes). The accompanying label reads: "South Australian Museum. Loc.: Sellicks Beach, Coll.: H.M. Hale, Date: 27/XII/1935, Depth: Reef. Tube-dwelling Amphipod. Like [?] lives in hollow fragments of *Cymodoce* [*Amphibolis*]". A separate small label in the vial reads: "*Siphonoecetes* + *Podocerus* sp., Sellicks, rock pools, 1936".

Although there is thus a slight discrepancy between the collecting date on the main label and the date stated by Sheard (1936), all other data are consistent with these specimens being Sheard's original material. As Sheard did not designate a holotype, I have selected a lectotype from this syntype series.

LECTOTYPE. Ovigerous female of 3.5 mm; South Australia, Gulf of St Vincent, Sellicks Beach, rock pool at Sellicks Reef, H.M. Hale, 27 December 1935; SAM C 2114.

PARALECTOTYPES., Five specimens, same data as lectotype, including: 1 ovigerous female, 2 ovigerous females without head, 1 young without head, 1 specimen in *Amphibolis* house; SAM C 4032.

Additional material examined (all previously unpublished). SOUTH AUSTRALIA. Fourteen specimens, Marino, Gulf of St Vincent, W. Baker, 1907 (identified as *Siphonoecetes australis* Stebb.), SAM C 2292; 28 specimens, including 1 in *Amphibolis* house, Marino, Gulf of St Vincent, Baker, 1910 (identified as variety of *S. australis*), SAM C 2293; 14 specimens in *Amphibolis* houses, Aldinga Reef, Gulf of St Vincent, 35°17′S 138°27′E, J.Window & M.McPhail, AM P31568; 3 specimens, South Australia, W.Baker, 1910, AM (Sheard collection) P35087; 1 specimen, Sellicks Beach, 35°20′S 138°27′E, H.M.Hale, 1936, AM (K. Sheard collection) P35092; 3 specimens, Marino Reef, Gulf of St Vincent, W.H. Baker & H.M.Hale, AM P35093; 6 specimens (2 with choniostomatid copepod parasite), Western River Cove, Kangaroo Island, 35°40′S 136°58′E, 5 m, algae, sheltered rocky shore, I.Loch, 1 March 1978, AM P34956.

NEW SOUTH WALES. Thirteen specimens in houses of plant material and/or light polychaete tubes, Maroubra Bay, Sydney, Haswell, 8 January 1899 (identified as *Siphonoecetes* n.sp.), AM P25461.

WESTERN AUSTRALIA. Two specimens, including 1 very large male, Cottesloe, Perth, L. Glaveri, 22 September 1923 (identified as *Siphonoecetes colletti* ? by C.Chilton 1957), AM P32000; 2 specimens, 2 km south-east of South Point, Two Peoples Bay, Albany, 34°58′S 118°12′E, 14 m, *Caulerpa* bases with sand, fine sand bottom, J.K.Lowry, WA-178, 16 December 1983, AM P34957; 1 specimen in *Amphibolis* house, northern side of Point John, Rockingham, 30 km south of Perth, 1.5 m, coarse sand with some detritus, immediately outside dense belt of *Amphibolis* and algae, hand dredge, J.Just, AU-5, 8 March 1984, ZMUC; 1 specimen in *Amphibolis* house, Frenchman Bay, King George Sound, Albany, western side of Waterbay Point, 0.75 m, coarse sand with *Halodule* surrounded by dense sea grass beds, hand dredge, J.Just, AU-21, 25 March 1984, ZMUC.

Description (mature females). Rostrum absent. Anterior margin of cephalon in dorsal view forming an angle of 90° or slightly more. Apex of eye lobes downward pointing in lateral view. Ventrolateral margins of cephalon curving strongly mediad.

Mouthparts: mandibular palp article 1 with 5–6 apical, pectinate setae, microsetulose lateral surface and a few short simple setae in proximal half. Outer plate of maxilla 1 with stout, blunt denticulate spines. Outer plate of maxillipeds with up to 14 stout medial spines, distal ones coarsely bilaterally dentate.

Antenna 1 reaching to about ⅔ the length of peduncular article 5 of antenna 2; peduncular article 1 subequal in length to article 2, article 3 ca. 75% the length of 2; peduncular article 1 with low, midlateral,

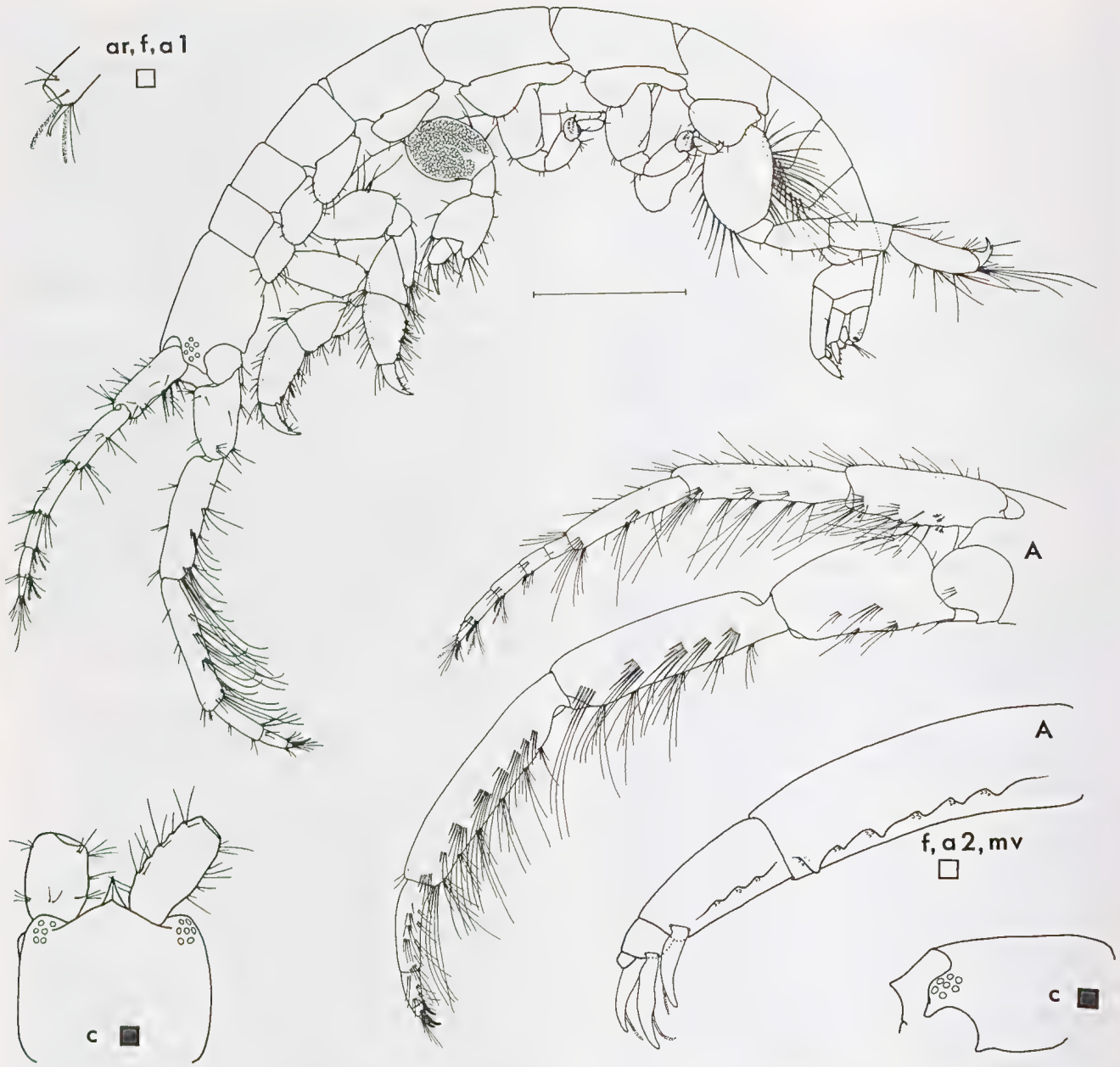

Fig. 3. *Australoecetes (Australoecetes) sellicki* (Sheard, 1936). Lectotype, except **A:** male of 8.0 mm, W.A. (AM P32000). Habitus scale: 0.5 mm.

longitudinal keel carrying 3–4 groups of spine-like setae (type 2, see Fig. 5), medial margin in dorsal view strongly scalloped with 5–6 groups of unequally long setae (type 2); flagellum as long as or up to 15% longer than peduncular article 2, with 4–6 articles, one or more (increasing with size of specimen) carrying ventromedial apical spine in addition to aesthetascs and setae. Antenna 2 as long as cephalon and first 4½–5½ pereonites combined; ventral projection of peduncular article 2 about as long as broad, with 1–2 apical setae; peduncular article 3 with groups of spine-like setae (type 2); articles 4 and 5 of equal length; article 4 dorsally with 2–4 groups of spine-like setae (type 1, see Fig. 5), laterally with 4–5 transverse groups consisting of 1 spine-like seta (type 1) and 1–4 (number increasing distally) long, curved, strongly plumose setae, ventrally with 4–6 groups of unequally long spine-like setae (type 2), medially with 6–7 transverse groups, proximal ones with slender spine-like setae (type 2), distal ones with 1 spine-like seta (type 2) and increasing number of long, curved, strongly plumose setae, distal most setae as long as peduncular article 5 and half of flagellum combined; article 5 armed as article 4 but generally with fewer groups of setae on respective surfaces, medial distalmost setae as long as flagellum; flagellum about 55% (large females) to 70% (small females) the length of

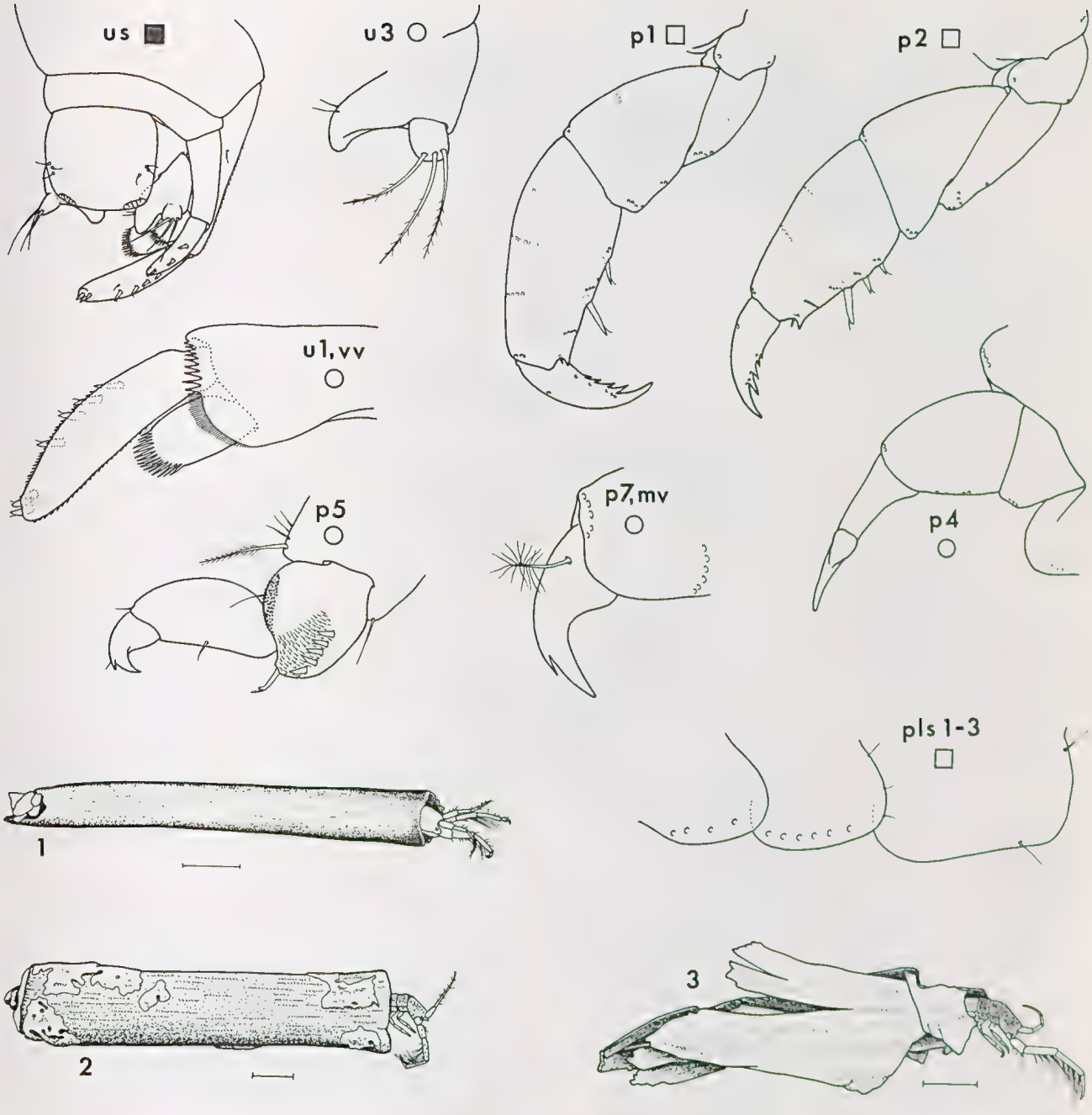

Fig. 4. *Australoecetes (Australoecetes) sellicki* (Sheard, 1936). Lectotype, except specimens in houses: **1** paralectotype; **2** specimen from W.A. (ZMUC, AU-5); **3** specimen from Maroubra Bay, N.S.W. (AM P25461); scales all 1 mm; **us** in oblique right view.

peduncular article 5, articles 2–4 combined ca. 65–70% the length of article 1, article 1 with lateral and medial long spine-like setae (type 1 and 2) and dorsal simple setae, article 2 laterally and medially with 2 spine-like setae (type 2) and distal simple setae, articles 3 and 4 with simple distal setae.

Coxal plates all broader than deep; plate 1 rounded rectangular; plate 2 lozenge shaped, anteriorly produced, with rounded apex; plate 3 more oval, anteriorly produced, with rounded apex, ca. 2.7 times broader than deep; plate 4 ca. 2.5 times broader than deep, broadly produced anteriorly, more narrowly produced posteriorly; plate 5 ca. 2.7 times broader than depth of anterior lobe, anterior lobe rounded triangular, with small rounded anteroproximal projection, posterior lobe narrow, roundedly produced backwards beyond posterior point of insertion of plate to posterior corner of peronite; plate 6 ca. 2.4 times broader than depth of anterior lobe, anterior lobe evenly rounded, plate otherwise as plate 5; plate 7 evenly rounded except for

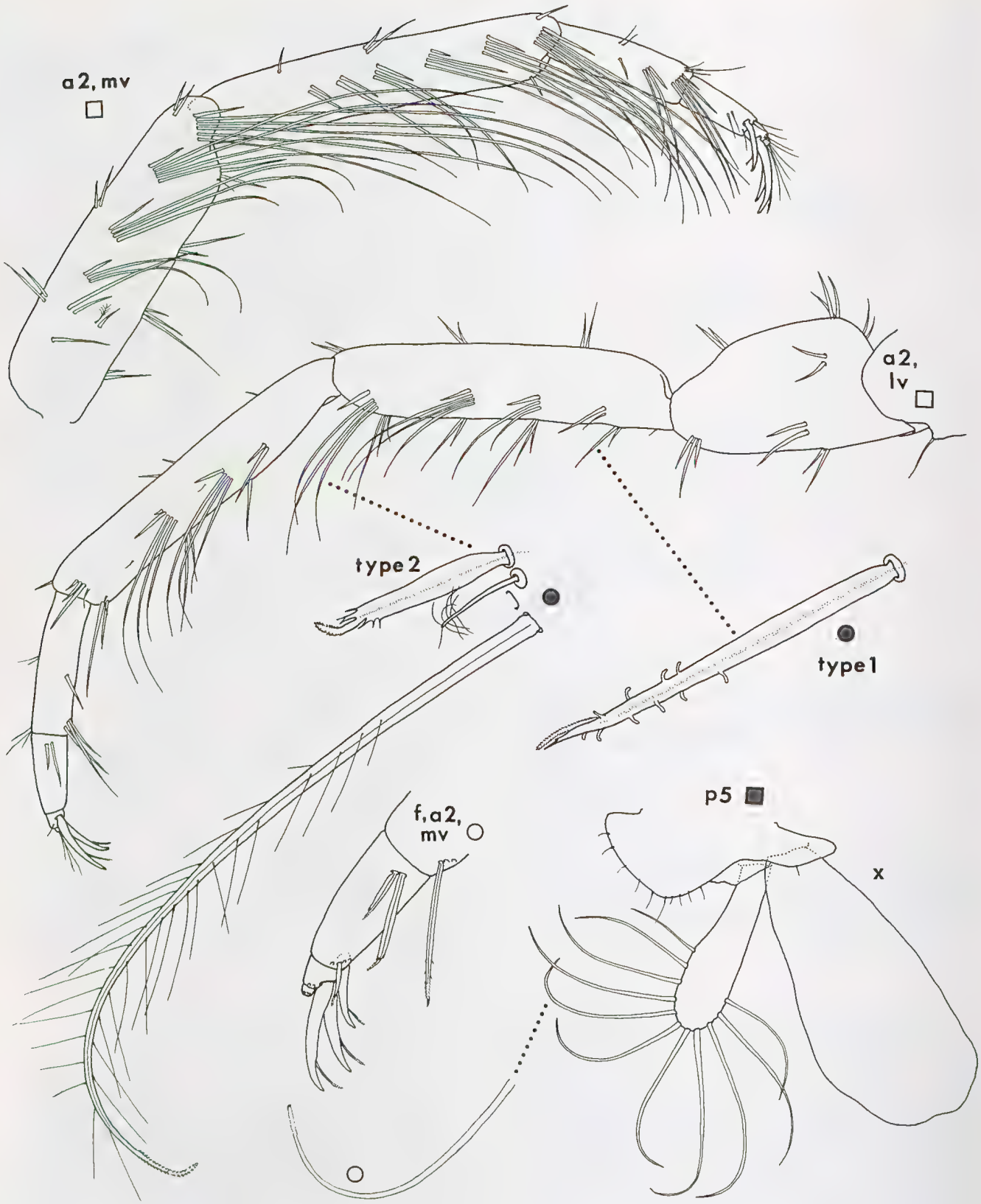

Fig. 5. *Australoecetes (Australoecetes) sellicki* (Sheard, 1936). Lectotype, except **X:** ovigerous female, S.A. (SAM C2293). Type **1** and **2** setae: see text.

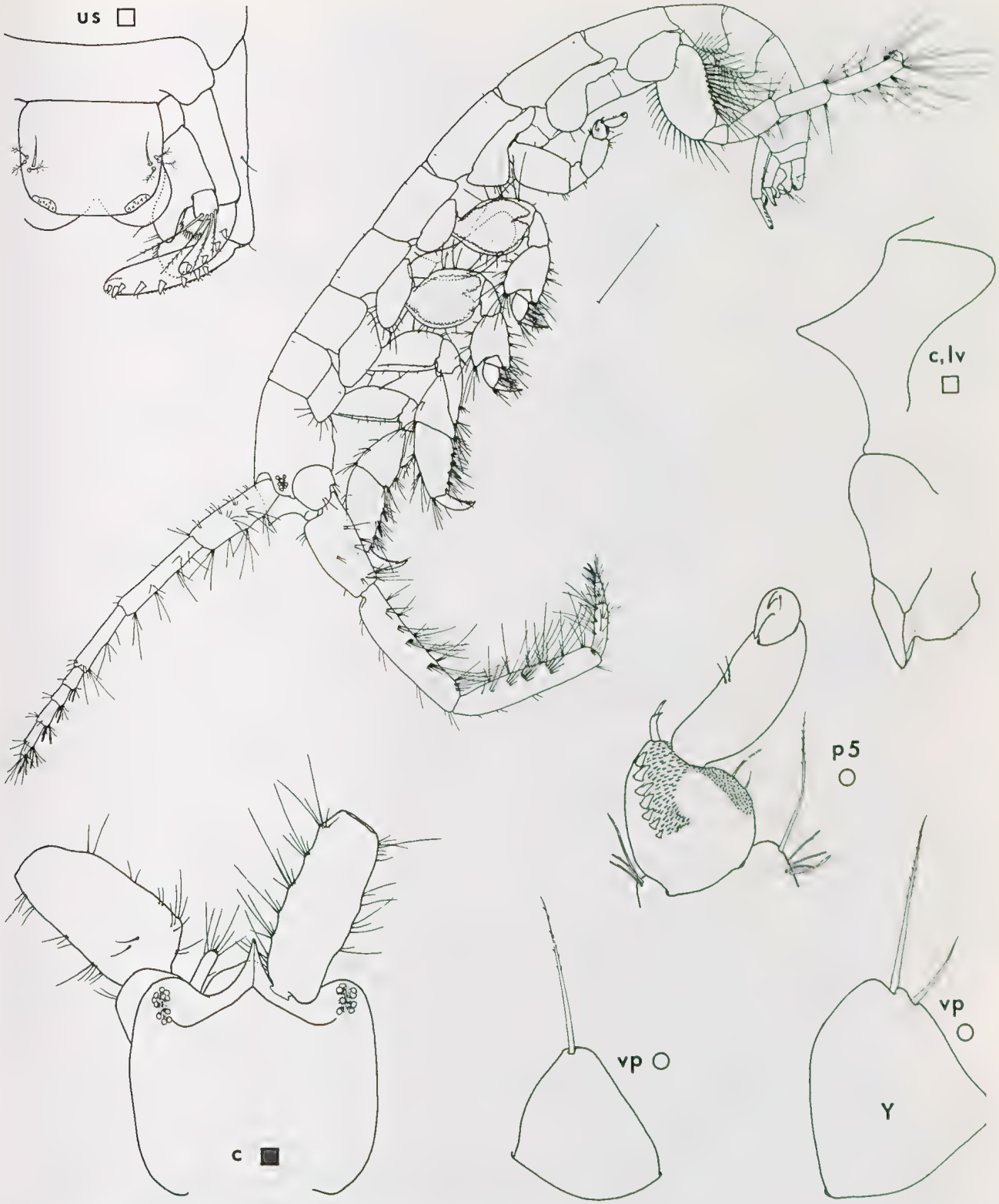

Fig. 6. *Australoecetes (Australoecetes) sellicki* (Sheard, 1936). Male of 4.4 mm, S.A. (AM P31568), except **Y**: male, S.A. (SAM C2293). Habitus scale: 0.5 mm.

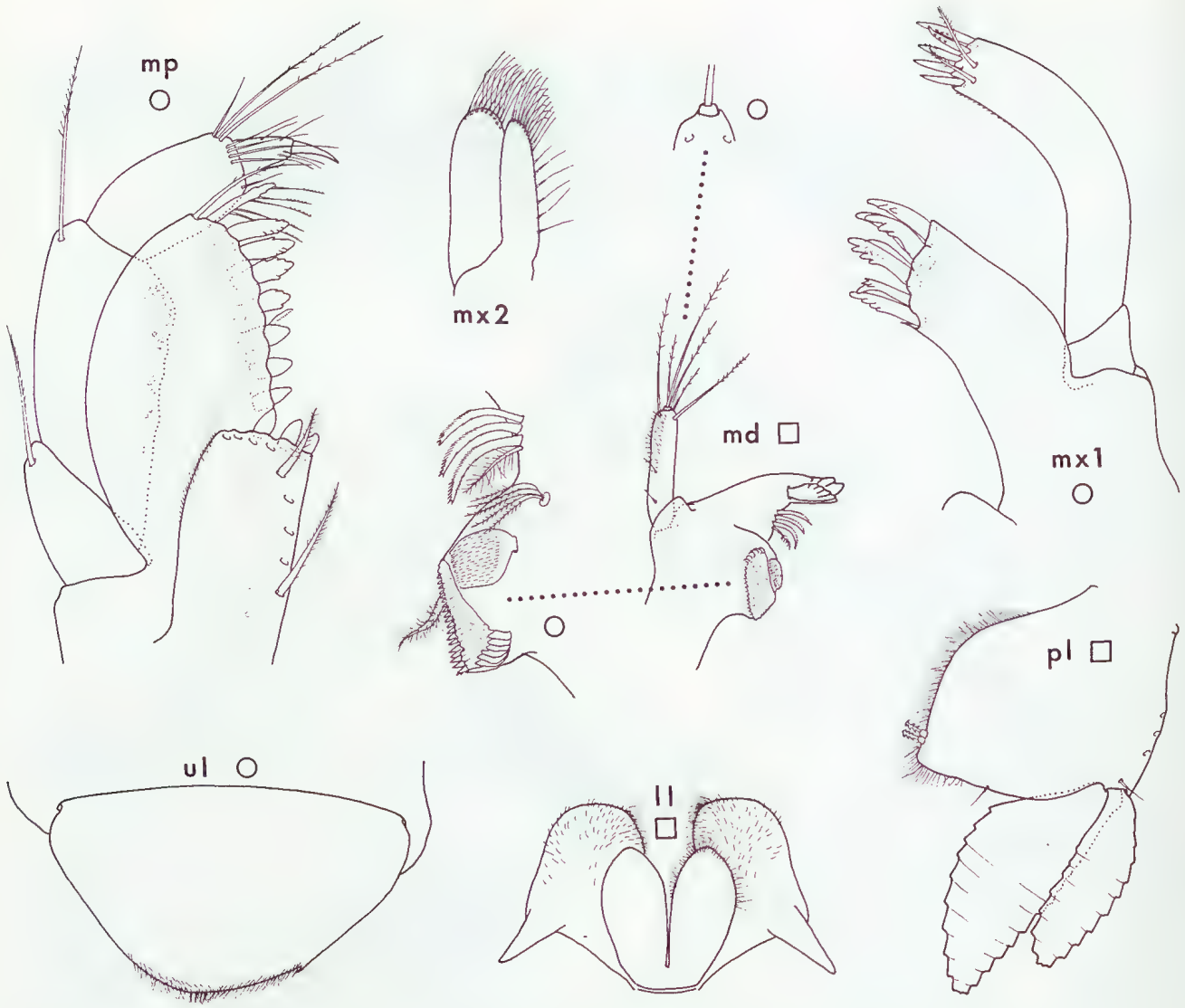

Fig. 7. *Australoecetes (Australoecetes) sellicki* (Sheard, 1936). Male of 4.4 mm, same specimen as in Fig. 6 (P31568).

posterior emargination and a small blunt proximal projection.

Pleonal sideplate 1 with up to 5, and plate 2 with up to 8, long plumose submarginal setae and a few short simple posterior setae, plate 3 with 1–2 short simple distoventral and 1 posterior setae.

Pereopod 1, article 6 oval, distally tapering, ca. twice as long as greatest width, with 2 midposterior spines. Pereopod 2, article 6 of similar shape but slightly broader than in pereopod 1, with 1 long midposterior and 2–3 short, more proximal spines. Pereopods 3–4, article 2 oval, 25–30% longer than broad, with 2–3 posterior groups of long setae. Pereopods 5–6, article 5 with lateral crecent of 5–7 short spines in addition to apical spine. Pereopod 7, dactylus with short (ca. ⅓ the length of dactylus: straight line between anterior point of insertion and tip of dactylus) plumose seta proximally on medial surface.

Uropod 1, peduncle reaching just beyond telson, lateral margin with 2–3 small setae, margin of ventroapical expansion with coarse acute denticles in lateral half, medial half with fine, closely set microsetules; outer ramus ca. ⅔ the length of peduncle (lateral margin), with 4–7 lateral spines in addition to apical group; inner ramus (excluding denticles) ca. 40% the lenght of outer ramus. Uropod 2 similar to 1, peduncle reaching apex of telson; outer ramus ca. 70% the length of peduncle, with 2–4 lateral spines in addition to apical spine. Uropod 3, peduncle strongly expanded mediocaudad, rounded apex produced byond tip of ramus, (the suction-like tip of the peduncular projection mentioned by Sheard 1936 does not exist; Sheard's interpretation must be due to an artificial folding in the specimen illustrated), mediodistal margin of peduncle with 3–4 short setae; ramus with 3–5 setae.

Telson rectangular with rounded corners, ca. 80% as long as broad.

Colour. Sheard (1936:451) writes: "... antennae ... orange, spotted with black; the body is slatey-grey to the fifth pereon segment, the remainder pallid". It is

not stated whether the colour was observed in live specimens or after a period of preservation.

Live animals observed by me in Western Australia had the base of article 1 of the peduncle of antenna 1 brown, antenna otherwise colourless transparent; antenna 2 in one specimen (AU-5) was colourless semitransparent, in another specimen (AU-21) with scattered brown blotches on peduncular articles 3–5.

Dark spots on antenna 2 can still be seen in many of the preserved specimens listed.

Cephalon, frontal cephalic surface (frons), mouthparts, and first 2 pereonites including coxae in the two W.A. specimens observed were dark brown, often in a reticulate pattern, the rest of the body increasingly light beige; appendages other than those mentioned were colourless transparent.

Size. Largest male: 8.0 mm; largest female: 5.5 mm; size range of mature females: 3.6–5.5 mm.

Sexual dimorphism. Males have longer and stouter, more densely setose antennae. Articles 1 and 2 of flagellum of antenna 2 in large males with strongly scalloped longitudinal ridge on medial surface (Fig.3)

Biology. The species lives in and around sea grass beds and algae. Over most of the range houses appear to consist exclusively of hollow stem nodes from *Amphibolis* sea grass (Fig. 4, **1–2**). No entrance tube is added to the house, but the posterior opening is covered with bits and pieces of algae and sea grass.

The material from Maroubra Bay (N.S.W.) was found in a different kind of houses (Fig. 4, **3**): empty, semitransparent polychaete tubes more or less covered with bits and pieces of algae and sea grass, or houses constructed from those materials without an inner polychaete tube; the posterior opening is covered in the above mentioned manner.

The implications of this difference in house building biology remain unclear until further material from the coast of south-eastern Australia can be studied.

The Western Australian specimens (AU–5, AU–21) were observed swimming rapidly with their house by strong downward beating with antenna 2, the long plumose setae of which can thus be ascribed a natatory function. Specimens also crawl slowly around on the sand or among the vegetation by aid of antenna 2.

Distribution. Southern parts of Australia from around Perth in the west to Sydney in the east; rock pools to 14 m depth.

Subgenus *Stebbingoecetes* n. subgen.

Diagnosis. *Australoecetes* without spines on flagellum of antenna 1. Peduncular articles 4 and 5 antenna 2 without transverse rows of long natatory setae. Inner ramus of uropods 1 and 2 with apical spine.

Description. Species assigned to this subgenus differ from *Australoecetes* s.s in the following points: Cephalon not markedly flattened, at most 10% longer than deep. Upper lip with notched apex and apical cuticular scales only. Mandibular palp relatively long, flattened (oval in cross section). Coxal plate 1 narrowly triangular, forward pointing. Pleopods with peduncle nearly twice as broad as long. Uropod 1, outer ramus with apical group of 1 long and 3 shorter spines; uropod 2, outer ramus with apical group of 2 short spines; inner ramus of uropods 1 and 2 with medial margin nearly straight, lateral margin convex, tapering distally towards blunt apex, margins in distal half denticulate.

Type-species. *Siphonoecetes australis* Stebbing, 1910.

Component species. *Australoecetes australis* (Stebbing, 1910), *Australoecetes jervisi* n.sp.

Australoecetes australis (Stebbing, 1910)
Figs 8–10

Siphonoecetes australis Stebbing, 1910: 619, pl. 54, all figs except C.

Australoecetes australis n. comb. — Just, 1983: 128.

Notes on type-material. Stebbing (1910) did not explicitly state how many specimens he had at hand, but he mentions a male (dissected: habitus and details illustrated) and an ovigerous female. The collecting localities given by Stebbing are: "Off Cape Three Points, 41 to 50 fathoms; and Botany Bay, from a depth of 50 to 52 fathoms".

The Australian Museum, Sydney, has two samples (AM P2529 and P2530) labeled *Siphonoecetes australis* Stebbing (original label), and marked syntypes at a later day. The label data are exactly as stated by Stebbing, and they represent 'Thetis' Expedition Stns 13 and 37 respectively.

P2529 (Cape Three Points) contains one fully developed female in a calcareous polychaete tube. P2530 (Botany Bay) contains two empty polychaete tubes and one fully developed female in a polychaete tube. Neither specimen has been dissected by Stebbing.

As mentioned by Just (1983: 128) these two specimens, which are undoubtedly part of Stebbing's original material, represent two different species in different siphonoecetine genera. P2530 belongs in *Australoecetes*, and the single specimen has accordingly been selected here as lectotype for *Siphonoecetes australis* Stebbing, 1910, (males belonging to this species agree with Stebbing 1910, pl. 54: all figs except C, which is from an undescribed species and genus). P2529 belongs in an as yet undescribed genus and represents an undescribed species (fig. C in Stebbing's above mentioned pl. 54).

A third sample in the collections of the Australian Museum, P31867 (re-registred from P2528), has exactly the same data as P2529. The single male present is most likely part of Stebbing's original material, but due to the lack of an original label it is not here treated as a syntype. The specimen belongs in the same undescribed species as P2529.

LECTOTYPE. Fully developed female of 3.3 mm, in polychaete tube. Botany Bay, New South Wales, 50–52 fathoms (91.5–95 m), 'Thetis' Expedition Stn 37; AM P2530 (old collection).

PARALECTOTYPES. None.

Additional material examined (all previously unpublished). Twenty-three specimens, including 1 in scaphopod and 5 in polychaete tubes, 33°52'S 151°23'E, 88 m, 2.5 m sledge-dredge, F.R.V. 'Kapala', K-80-20-11, R.T. Springthorpe & P. Colman, 11 December 1980, AM P32002 and P35730 (male A), except 1 male and 1 female: ZMUC; 1 specimen, 40°13.8'S 148°39.6'E, Bass Strait east of Flinders Island, 60 m, fine sand,

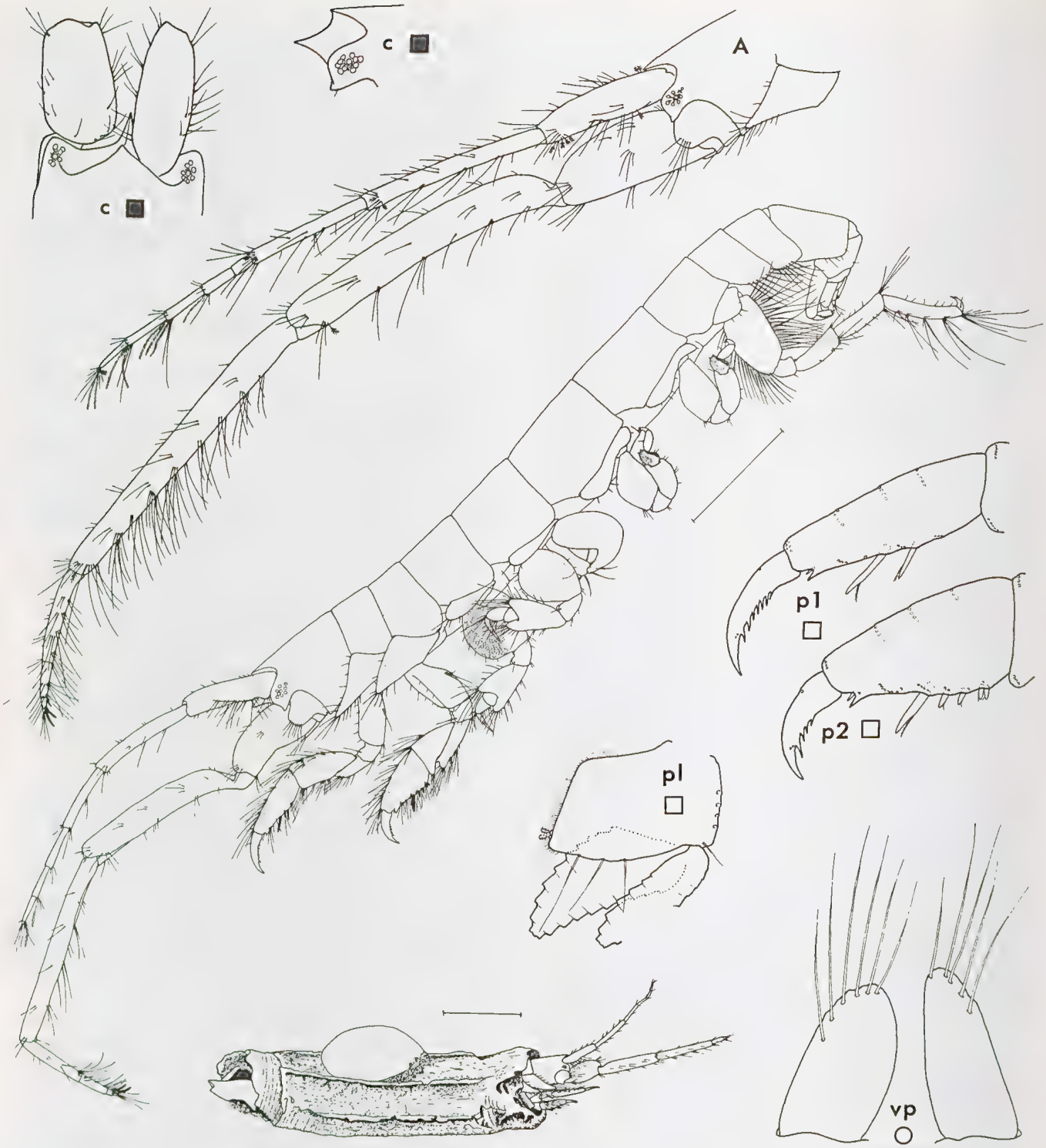

Fig. 8. *Australoecetes (Stebbingoecetes) australis* (Stebbing, 1910). Lectotype, except **A**: male of 4.3 mm (AM P35730). Habitus scale (including **A**): 0.5 mm. Scale for animal in house: 1 mm.

epibenthic sled, NMV Bass Strait Survey Stn BSS 165, cruise 81-HK-1, 14 November 1981, NMV J2636; 25 specimens, 39°44.8′S 148°40.6′E, Bass Strait east of Flinders Island, 124 m, muddy sand, epibenthic sled, NMV Bass Strait Survey Stn BSS 167, cruise 81-HK-1, 14 November 1981, NMV J9525.

Description (mature females). Rostrum in lateral view a short point. Apex of eye lobes forward pointing in lateral view. Ventrolateral margins of cephalon only faintly inward curving.

Mouthparts: mandibular palp article 1 ca. 3 times longer than broad in the middle, somewhat tapering in distal half, ventral margin with 4–5 transverse groups of long pectinate setae, medial surface with 3–4 short stiff setae single or in pairs and 2 unequally long

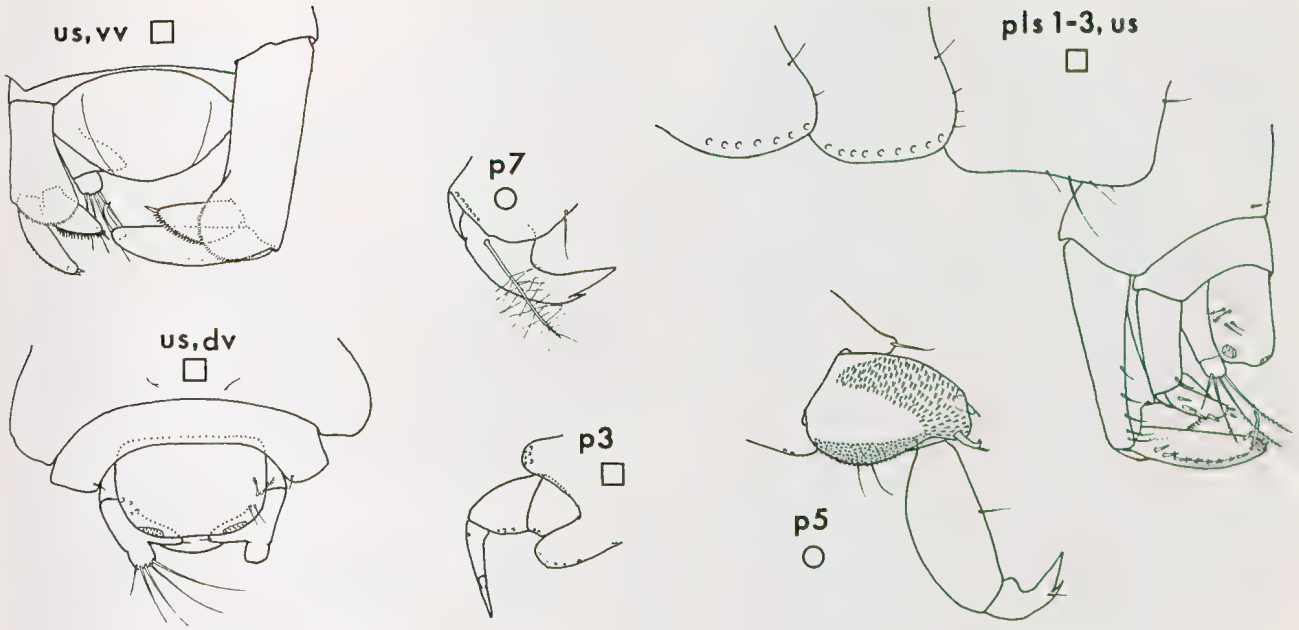

Fig. 9. *Australoecetes (Stebbingoecetes) australis* (Stebbing, 1910). Lectotype.

subapical setae. Outer plate of maxilla 1 with slender, acute, bi- or trifid spines. Outer plate of maxillipeds with up to 9 medial spines, distal ones long, slender, acute, unilaterally denticulate.

Antenna 1 as long as cephalon and first 4–4½ pereonites combined, reaching to about the middle of peduncular article 5 of antenna 2; peduncular article 2 ca. 8 times longer than broad, 18–20% longer than article 1 and 58–60% longer than 3, article 1 with low lateral keel carrying row of long setae, medial margin in dorsal view smooth with 5–6 groups of setae; flagellum with 3–4 slender articles, article 3 ca. 6.5 times longer than broad. Antenna 2 ca. as long as cephalon and entire pereon combined, slender, sparsely setose; lateral surface of peduncular article 1 with transverse row of setae; ventral projection of peduncular article 2 nearly twice as long as broad at base, with 5–6 long setae apically and distolaterally; article 3 distally tapering, proximal half of dorsolateral surface with a few setae only; articles 4 and 5 of equal length; article 5, 11–12 times longer than broad; flagellum ca. half the length of peduncular article 5, articles 2–4 combined ca. 65% the length of article 1.

Antennal setae all short, slender, distally micropectinate (Fig. 10,s), occasionally with coarser pectination more proximally.

Coxal plate 1 narrowly triangular, acute, forward pointing, anterior margin 80–100% longer than plate width at base; plate 2 of similar shape but less narrowly triangular, apex blunt, anterior margin ca. 25% longer than width at base; plates 3 and 4 ca. 3 and 4.5 times broader than deep respectively, anteriorly rounded, posteriorly strongly tapering, plate 3 more anteriorly produced than 4; plates 5 and 6 ca. 3 times broader than depth of anterior lobe, anterior lobe broader and slightly deeper than posterior lobe, posterior lobe in plate 5 rounded, in plate 6 posteroventrally produced into a blunt point.

Pleonal sideplate 1 with 6–7 long plumose submarginal setae and 2 short posterior setae; plate 2 with 8–9 plumose setae and 3–4 short posterior setae; plate 3 with 4–5 unequally long simple setae along posterior ⅓ of ventral margin and 1–2 posterior setae.

Pereopod 1, article 6 slender, ca. 3 times longer than greatest width, with 2 slender midposterior spines; articles 5 and 6 of equal length. Pereopod 2, article 6 oval, distally tapering, ca. twice as long as greatest width, with 1 long midposterior spine and 3–4 smaller proximal spines; article 5 ca. 80% the length of article 6. Pereopods 3–4, article 2 oval, ca. 20% longer than broad; article 2 in pereopod 3 with 1–2 long posterior setae, such setae absent in pereopod 4. Pereopods 5–6, article 5 with 1 short subapical spine in addition to apical spine. Pereopod 7, dactylus with long (ca. 80% the length of dactylus, see *Australoecetes sellicki*), dense plumose seta proximally on medial surface.

Uropod 1, peduncle reaching beyond telson with ca. ⅓ of its length, distal half of lateral margin with 4 stout setae, ventral apical expansion covering ½ inner, ⅓ of outer ramus, margin of expansion fringed with microsetules; outer ramus ca. 70% the length of peduncle (lateral margin), with 7–9 lateral spines addition to apical group; inner ramus ca. half as long as outer ramus. Uropod 2 similar to 1; peduncle reaching ca. ⅚ along peduncle of uropod 1, distolateral margin with 2–3 stout setae; outer ramus ca. as long as peduncle, with 3–4 lateral spines in addition to apical group; inner ramus ca. ⅔ the length of outer ramus. Uropod 3, peduncular expansion directed mediad, with 2–3 short apical-subapical medial setae; ramus with 4–5 pectinate setae.

Telson ca. 50% broader than long, of rectangular

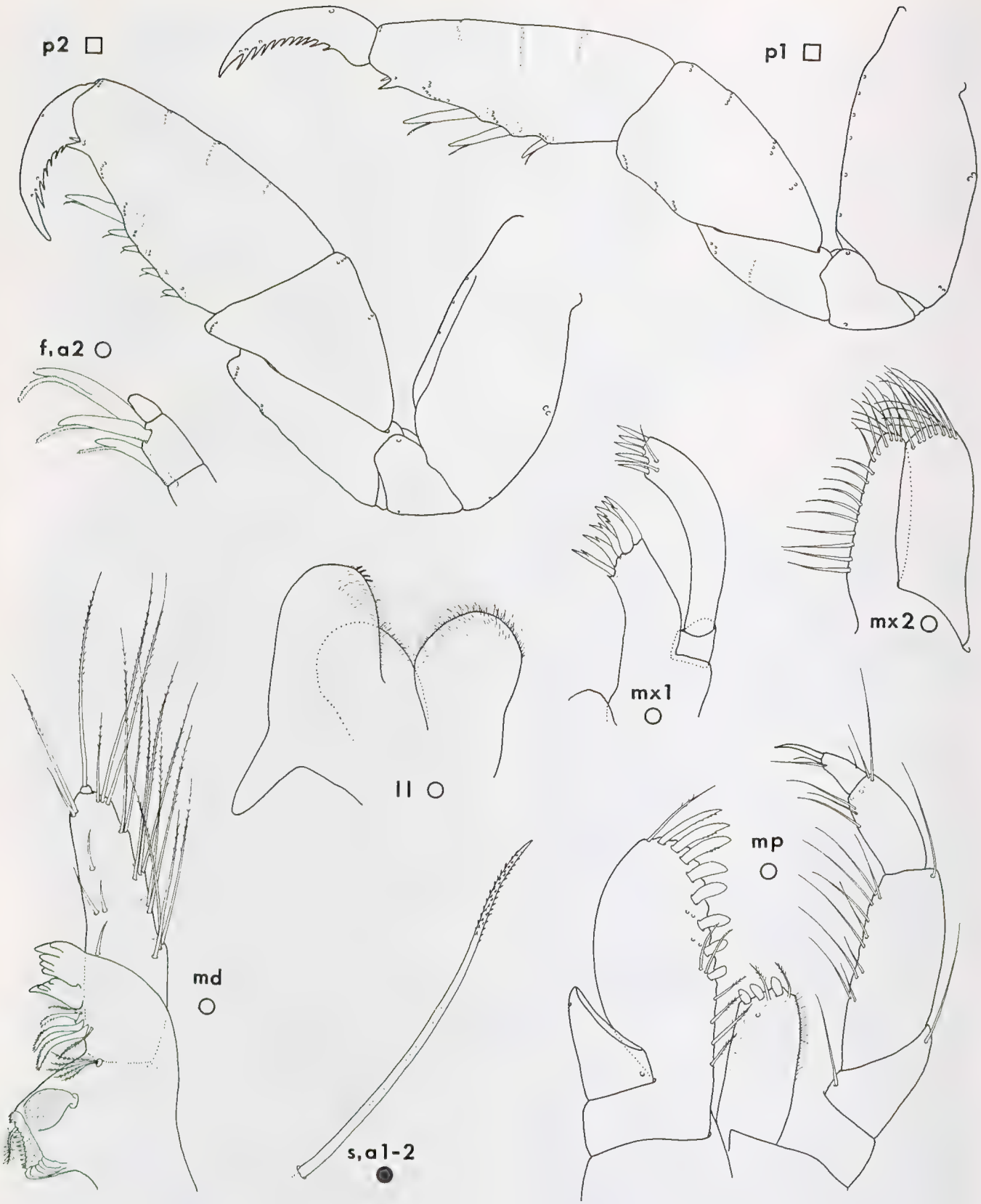

Fig. 10. *Australoecetes (Stebbingoecetes) australis* (Stebbing, 1910). Male of 4.3 mm, same specimen as A in Fig. 8.

shape, distal corners evenly rounded, apical margin nearly straight.

Colour. Not known. Several specimens in the AM P32002 sample have a dark, longitudinal core in the antennae (cf. the following species).

Size. Largest male: 4.3 mm; largest female: 3.6 mm; size range of mature females: 2.8–3.6 mm.

Sexual dimorphism. Antennae longer in males. Antenna 1 with up to 6 flagellar articles; peduncular article 2 ca. 33% longer than 1 and ca. 45% longer than 3. Antenna 2 in large males as long as cephalon and entire pereon and pleon combined; peduncular article 5 with about twice as many groups of ventral setae; flagellum ca. 40% the length of peduncular article 5, articles 2-4 combined ca. 55% the length of 1.

Pereopod 1 in large males with article 5 ca.80% the length of article 6, in pereopod 2 ca. 65% the length of article 6.

Coxal plates 1 and 2 of similar shape but shorter in relation to width than in females; plate 3 more pointedly produced anteriorly.

Biology. The species has been found on fine sand, and on muddy sand (64% sand, 34% silt and mud, pers. comm. Dr Gary Poore, BSS St. 167).

Of the 50 specimens treated seven were still in their house (1 in small scaphopod, 6 in more or less straight pieces of calcareous polychaete tubes, Fig. 8). There is no sediment-grain entrance tube attached to the houses, but a small tube (cf. the following species) may have been torn off during dredging operations. The posterior opening is loosely covered with small shell fragments.

Distribution. South-eastern Australia, Bass Strait to Sydney; between 60 and 124 m depth.

Australoecetes jervisi n. sp.
Figs 11–13

Type-material. HOLOTYPE. Male of 3.8 mm in calcareous polychaete tube, Jervis Bay, New South Wales, south-east of Huskisson off Moona Moona Creek, 35°03'S 150°52'E, 8 m, along inner edge of low rock reef, fine sand with detritus, hand dredge, SCUBA, J.Just, P.B. Berents, R.T. Springthorpe, AU-68, 16 November 1984, AM P35731.

PARATYPES. Ten specimens in calcareous polychaete tubes and scaphopods, same data as holotype, AM P35732 (5 specimens) and P35733 (paratype A, ovigerous female), 4 specimens in ZMUC; 5 specimens in similar houses, same data as holotype except: AU-65, 15 November 1984, ZMUC.

Description (adult males). Rostrum in lateral view a short point. Apex of eye lobes forward pointing in lateral view. Ventrolateral margin of cephalon only faintly inward curving.

Mouthparts closely similar to *A. australis*. Mandibular palp with three transverse rows of setae on ventral margin (the two posterior rows in right mandible of holotype forming continuous oblique transverse crescent, Fig. 12). Outer plate of maxillipeds with up to 10 medial spines.

Antenna 1 as long as cephalon and first 4–4½ pereonites combined, reaching ⅔ along peduncular article 5 of antenna 2; peduncular article 2, 5–5½ times longer than broad, ca. 10% longer than article 1 and ca. 45% longer than 3; article 1 with low lateral keel carrying 3–4 groups of long setae, medial margin in dorsal view smooth with 5–6 groups of setae; flagellum 10–12% longer than peduncular article 2, with 4–5 articles, article 3 ca. 3.5 times longer than broad. Antenna 2 as long as cephalon and first 6–6½ pereonites combined; lateral surface of peduncular article 1 with transverse row of setae; ventral projection of article 2 about as long as broad or slightly longer, triangular with broadly rounded apex and 2–4 apical and distolateral setae; article 3 barely tapering distally, proximal half of dorsolateral surface with 4–5 irregular transverse rows of setae (2–4 setae in each row); article 4 with 4–5 groups of ventral setae; article 5, 6½–7 times longer than midwidth, with 7–8 irregular groups of ventral setae; article 5 ca. 17% longer than 4; flagellum 50–55% the length of peduncular article 5, articles 2–4 combined ca. 58% the length of article 1.

Antennal setae similar to those in *Australoecetes australis* (Fig. 10,s).

Coxal plate 1 narrowly triangular, acute, forward pointing, anterior margin as long as plate width at base; plate 2 of similar shape but less narrowly tapering, anterior margin slightly convex, ca. 85% the length of plate width, apex rounded; plate 3 triangular, forward pointing with broadly rounded apex, anterior margin ca. 80% the length of plate width; plate 4 broadly rounded anteriorly, posteriorly tapering towards rounded corner, ca. 2.5 times broader than deep; plate 5 ca. 3.5 times broader than depth of anterior lobe, anterior lobe rounded triangular, posterior lobe posteroventrally produced with rounded apex, lobes of subequal depth; plate 6 ca. 4 times broader than depth of anterior lobe, anterior lobe evenly convex, posterior lobe posteroventrally produced, tapering towards bluntly pointed apex, slightly deeper than anterior lobe.

Pleonal sideplate 1 with 4–5 long plumose submarginal setae and 1 small posterior seta; plate 2 with 5–6 plumose setae and 2–3 small posterior setae; plate 3 with 2–3 unequally long simple setae along posterior ⅓ of ventral margin and 1–2 posterior setae.

Pereopod 1, article 6 tapering in distal half, ca. 2.2 times longer than greatest width, with two long, midposterior spines; article 6 ca. 15% longer than 5. Pereopod 2, article 6 broadly oval, ca. 1.8 times longer than greatest width, with 1 long midposterior spine and 3 smaller spines more proximally; article 6 ca. 40% longer than 5. Pereopods 3–4, article 2 nearly circular (7–8% longer than broad); article 2 in pereopod 3 with 1–2 long posterior setae, such setae absent in pereopod 4. Pereopods 5–6, article 5 with 1 short subapical spine in addition to apical spine. Pereopod 7, dactylus with long (ca. 80% the length of dactylus) densely plumose seta proximally on medial surface.

Uropod 1, peduncle reaching beyond telson with ca. ⅓ its length, distal half of lateral margin with 4–5 stout setae, ventral apical expansion covering about half of

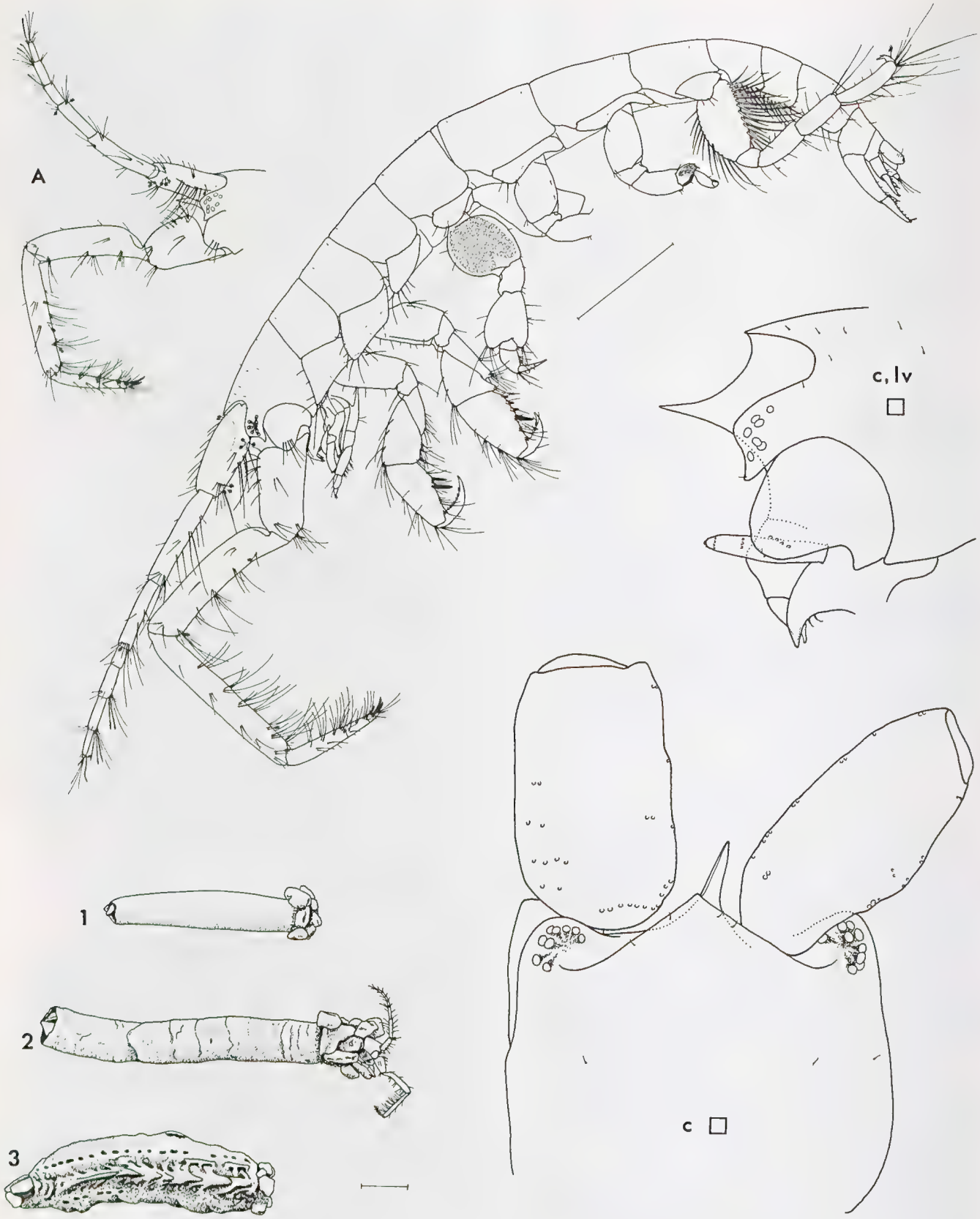

Fig. 11. *Australoecetes (Stebbingoecetes) jervisi* n. sp. Holotype, except **A**: female paratype **A**, 3.8 mm (AM P35733), and **1** and **3**: both from type locality. Habitus scale (including **A**): 0.5 mm. Scale for houses: 1 mm.

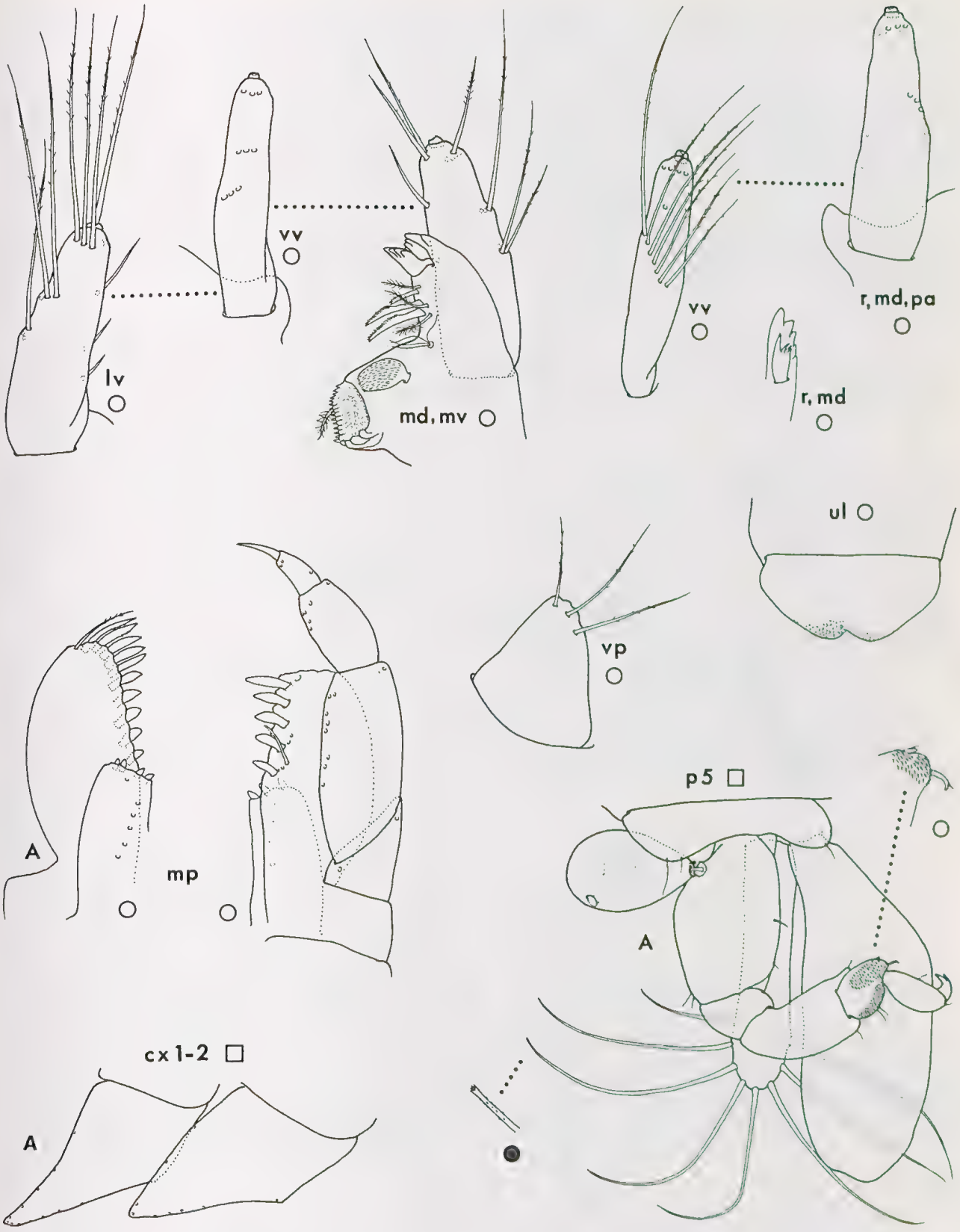

Fig. 12. *Australoecetes (Stebbingoecetes) jervisi* n. sp. Holotype, except **A**: female paratype **A** (see Fig. 11). Apex of outer plate in holotype maxilliped damaged. Note ectoparasite in female **A** pereopod 5.

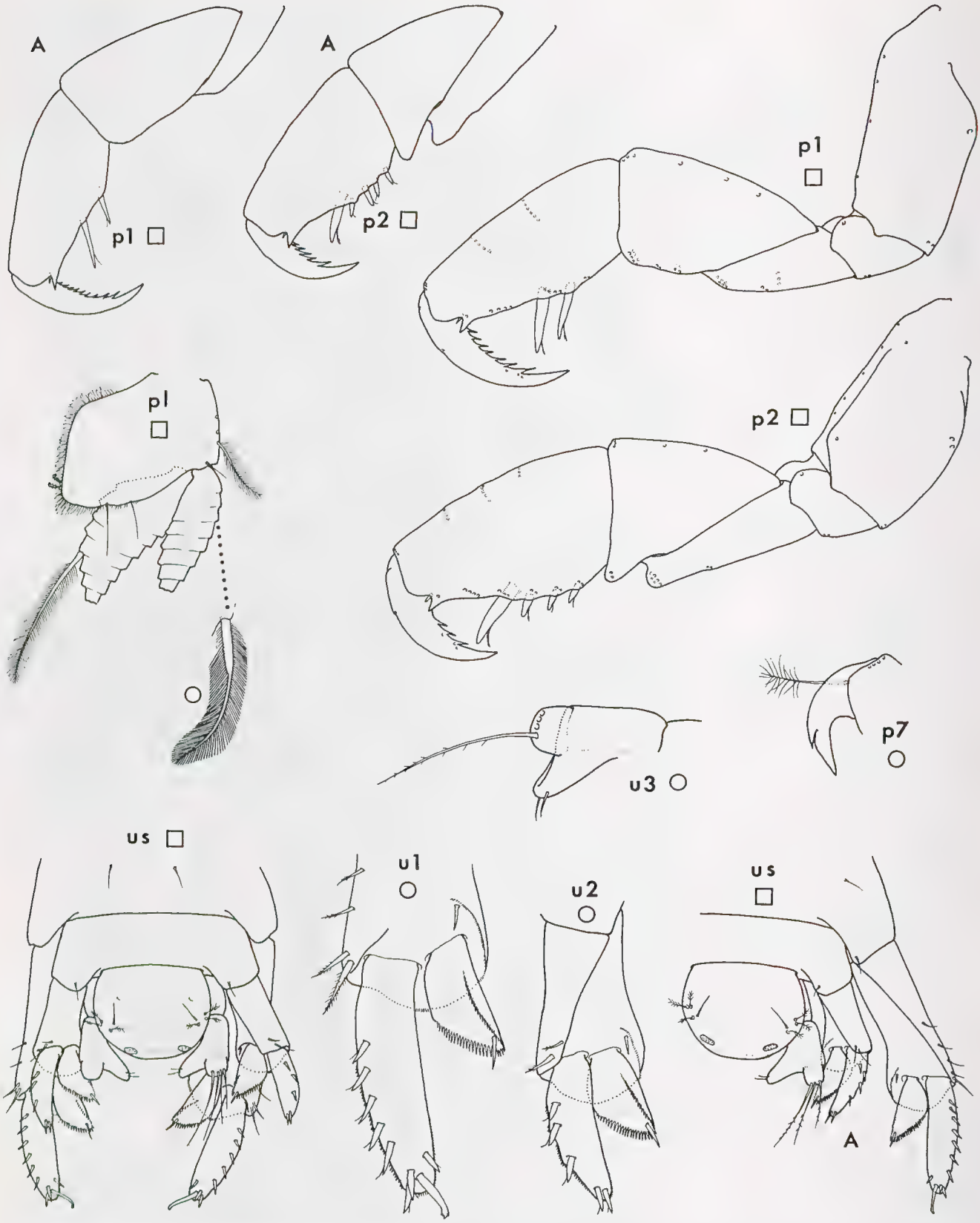

Fig. 13. *Australoecetes (Stebbingoecetes) jervisi* n. sp. Holotype, except **A**: female paratype **A** (see Fig. 11).

inner and ⅕ to ⅙ of outer ramus, margin fringed with microsetules; outer ramus ca. 60% the length of peduncle (lateral margin), with 5–7 lateral spines; inner ramus half as long as outer ramus. Uropod 2 similar to 1; peduncle reaching ca. ¾ along peduncle of uropod 1, distolateral margin with 2 stout setae, ventral expansion covering ½ of inner, ca. ⅓ of outer ramus; outer ramus ca. as long as peduncle, with 2–3 lateral spines; inner ramus ca. ⅔ the length of outer ramus. Uropod 3, peduncular expansion directed mediad, with 2–3 short subapical setae; ramus with 3–4 setae.

Telson ca. 25% broader than long, with convex lateral margins curving evenly into slightly less convex apical margin.

Colour (live animals). Cephalon and first two pereonites mottled brown, pereonites 3–7 mottled with white pigment, brown entrails shining through, pleon and urosome semitransparent. Eyes white with black ocelles. Frons pale brown. Antenna 1 colourless transparent, but peduncular articles 1 and 2 with central, longitudinal, cylindrical, red-brown core. Antenna 2, peduncular articles 3–4 (female) or 3–5 (male) with similar but weaker central core, peduncular articles 3-5 with pale yellow-white apical ring, antenna otherwise colourless transparent. Mouthparts with brownish tinge, all other body appendages colourless transparent.

Size. Largest male: 3.8 mm; largest female: 3.8 mm; size range of mature females: 3.0–3.8 mm.

Sexual dimorphism. Females have shorter and somewhat less setose antennae: antenna 1 as long as cephalon and first 2½–3 pereonites combined, antenna 2 as long as cephalon and first ca. 4½ pereonites combined; peduncular article 2 of antenna 1 subequal to 1, 50–55% longer than 3, flagellum as long as peduncular article 2, with 3–4 articles; antenna 2, peduncular article 3 distinctly shorter in relation to width than in male, article 5 ca. 10% longer than 4, flagellum ca. 60% the length of peduncular article 5, articles 2–4 combined ca. 60% the length of 1.

Coxal plates 1 and 2 longer and more pointed than in male, anterior margin of 1 ca. 80% longer than plate width at base, of 2 ca. 35% longer; plate 3 less produced with anterior corner more angular.

Pereopod 1, articles 5 and 6 of equal length; pereopod 2, article 6 ca. 12% longer than 5, with up to 4 short posterior spines proximal to large midposterior one.

Uropod 2 with inner ramus up to ¾ the length of outer ramus.

Biology. The species was taken on fine sand with detritus in relative shelter along the landwards foot of low stone reefs, within 1 metre of the reef. Further landwards, at similar depths, in more exposed conditions with slightly coarser sediments where large numbers of other siphonoecetines occurred, *A. jervisi* was not observed.

The 14 specimens were all found to inhabit rather straight houses (scaphopods, calcareous polychaete tubes, Fig. 11), to which is added a very short entrance tube of sand grains or shell fragments, often a single tier only; the posterior opening is loosely covered with shell fragments.

The specimens crawled slowly around primarily by aid of antenna 2. The backward jumping movement typical of many siphonoecetines was never observed.

Distribution. Jervis Bay, New South Wales; eight metres.

Remarks. Although closely similar to *A. australis*, *A. jervisi* can be readily distinguished from that species by its shorter and more compact antennae in which the length/width ratio of articles is distinctly less than in *A. australis*.

ACKNOWLEDGEMENTS. The present study is part of the results obtained during 10 months work in Australia, primarily funded by the Danish Natural Sciences Research Council (SNF 11-4180) and the Carlsberg Foundation, Copenhagen. The Australian Museum, Sydney, is gratefully thanked for supporting field work in Jervis Bay and visits to Melbourne and Adelaide. In the present context it is a pleasure to thank Mr Roger T. Springthorpe (collection manager, AM) for help and advice with the AM collections. Mrs Penelope P. Berents (AM) and R.T. Springthorpe made it possible for me to dive in Jervis Bay to observe and collect the rich fauna of siphonoecetines. I thank Dr Gary Poore (Museum of Victoria) and Mr Wolfgang Zeidler (South Australian Museum) for hospitality and access to unpublished collections and type material.

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The Anatomy and Relationships of *Emblanda emblematica* (Hedley) (Mollusca: Mesogastropoda: Emblandidae n.fam.)

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ABSTRACT. A new monotypic family is created for *Emblanda emblematica* (Hedley), a minute rissoacean gastropod from south- eastern Australia. It is unique in the Rissoacea in possessing a triseriate radula and a penial sheath behind the hypobranchial gland. The alimentary canal is modified for specialized feeding on Foraminifera, especially the wide, simple oesophagus, the spacious stomach with an elongate posterior chamber and the very reduced crystalline style. The female has a glandular section of the oviduct behind the albumen gland, which is of importance in separating *Emblanda* from the related family, Barleeidae.

PONDER, W.F., 1985. The anatomy and relationships of *Emblanda emblematica* (Hedley) (Mollusca: Mesogastropoda: Emblandidae n.fam.). Records of the Australian Museum 37(6): 343-351.

KEYWORDS: *Emblanda*, Emblandidae, Rissoacea, anatomy, radula.

Convergence in minute gastropods has proved to be one of the main problems in achieving a reliable classification. Historically shell characters have been used as the primary means of classification but, in many cases, where the much larger numbers of characters available from anatomical studies have been used to test these classifications, they have been shown to require considerable modification.

The minute, marine gastropod that is the subject of this paper has a shell very similar in appearance to that of some members of the Barleeidae (see Ponder, 1984) and Rissoidae (see Ponder, 1985). An examination of the radula, however, showed it to be very unusual. An anatomical investigation was carried out to establish the relationships of this otherwise rather undistinguished species.

Emblanda emblematica, the only known species of *Emblanda*, is a tiny, rare, prosobranch snail found living in algae in the lowest littoral and shallow sublittoral zones in New South Wales, Australia. It has been mentioned only occasionally in the literature. Hedley (1906), when he first described the species thought it was related to the '*Rissoa cheilostoma* group' (i.e. genus *Merelina*, Rissoidae), a suggestion also made by Laseron (1956). Iredale (1924) placed it in *Anabathron*. Iredale (1955: 81) later introduced a new generic name for this species stating that it differed from *Anabathron* 'in size, coloration and mouth-features I have recently indicated that a new family-group taxo might be required for *Emblanda* (Ponder, 1985).

The present account is incomplete, particularly regarding some aspects of the female genital system, mainly because of the small number of specimens available for study. The available material is all that has accumulated over the last fifteen years of collecting micromolluscs in New South Wales. Nonetheless the information presented below is sufficient for a reasonable estimate of the relationships of this genus.

Material and methods.

The methods used for radular extraction and mounting are given by Ponder & Yoo (1976). Mounts of five radulae were prepared, one being accidentally mounted upside down. Six specimens were fixed in Bouin's fluid and embedded in paraffin. Serial sections were cut at about 4-6 mm and stained with Mallory's triple stain. Three male specimens were dissected but, mainly because of the small size of this animal, the dissections were not very useful; most of the anatomical information has been ascertained from serial sections. No female specimens have been available for dissection and only one mature and two immature females have been sectioned.

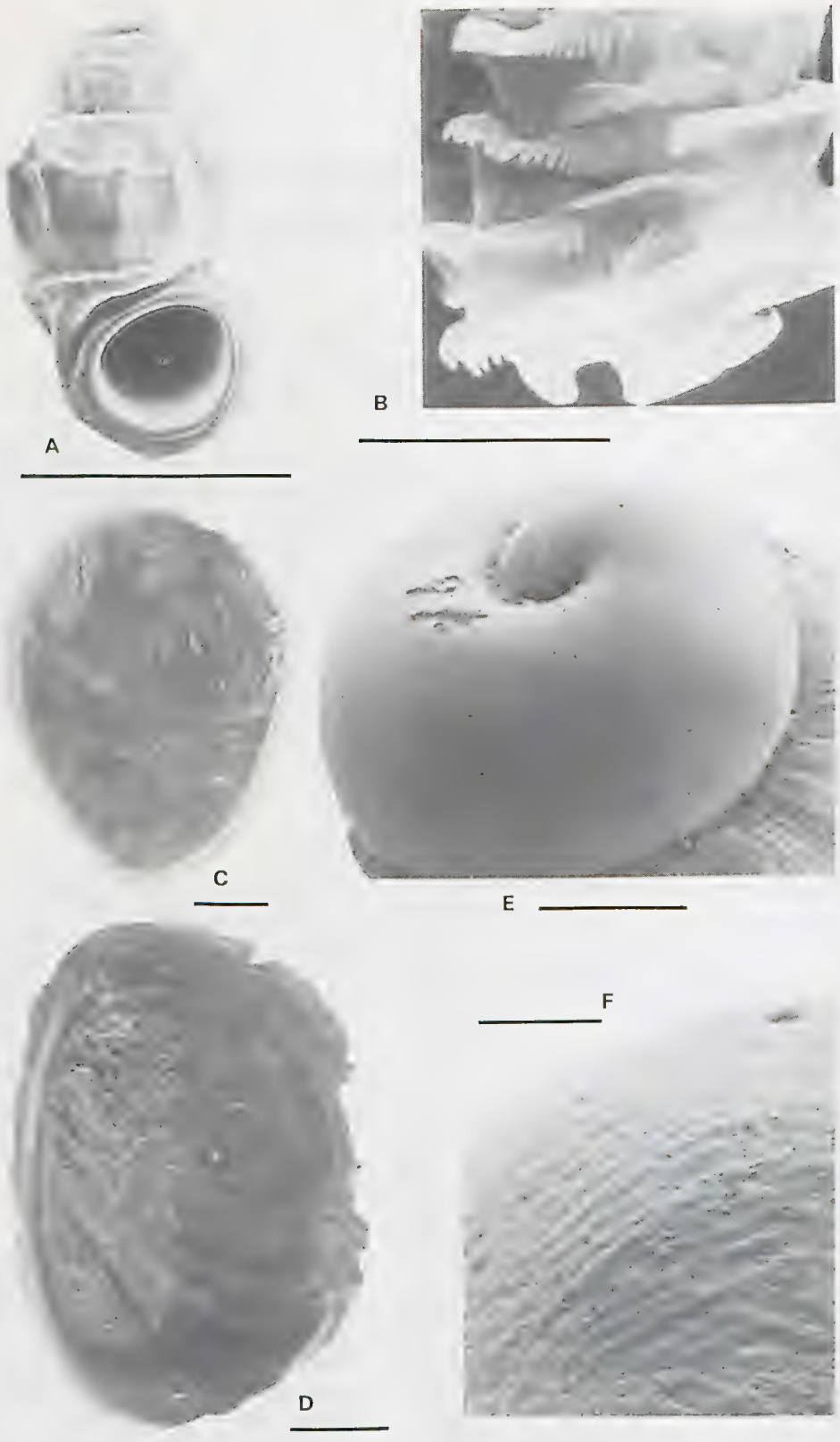

Fig. 1. **A:** Shell. **B:** Radula. **C, D:** Operculum; **C,** outer side, **D,** inner side. **E, F:** Protoconch; **F,** microsculpture. **Scales:** A, 1mm; B,F, 0.01mm; C-E, 0.1mm. A-C, Batehaven, Batemans Bay, N.S.W.; D-F, Fingal Head, Port Stephens, N.S.W.

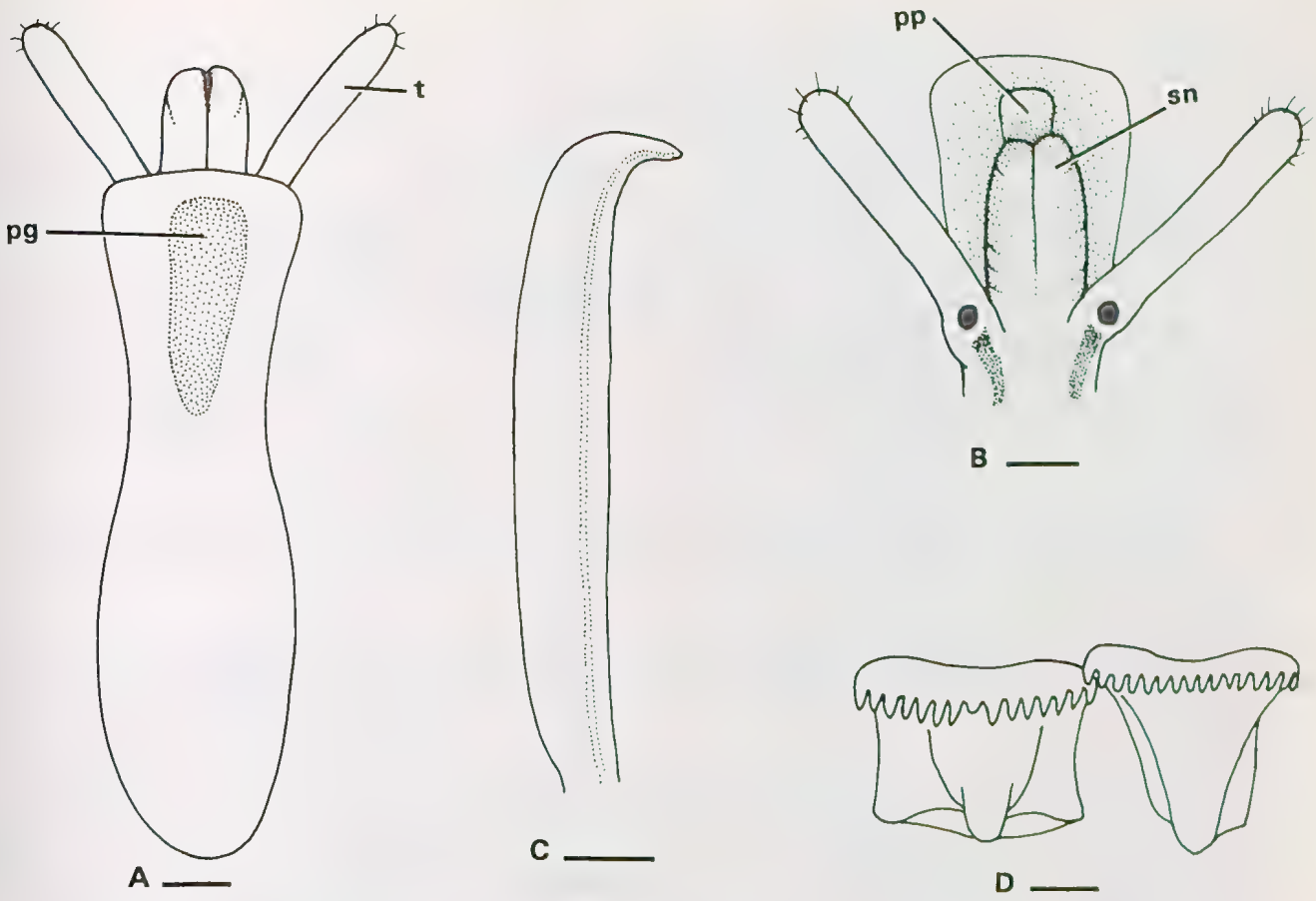

Fig. 2. Head-foot. **A:** Ventral view of head-foot. Opercular lobe and operculum not shown. **B:** Dorsal view of head and anterior foot. **C:** Penis. **D:** A diagrammatic representation of the central and one lateral radular tooth. **pg,** anterior pedal gland; **pp,** propodium; **sn,** snout; **t,** cephalic tentacle. **Scales:** A-C, 0.1mm; D, 0.001mm.

Description

Shell (Fig. 1A, E, F). The shell is minute (adults range from 1.47 to 2.03 mm in length), solid and non-umbilicate. There is a thin, dark red to colourless, inner chitinous layer present (see Ponder & Yoo, 1976). The protoconch (Fig. 1E, F) of about 1¼ whorls, is dome-shaped, the first half whorl minute and tilted. It is sculptured with spirally-aligned irregular wrinkles and the whole surface is covered with extremely minute, shallow pits (Fig. 1F). The teleoconch consists of 2 to 3 whorls and is sculptured with strong axial ribs (about 10–12 on the body whorl) which are angulated and nodulose where crossed by a prominant spiral cord on the periphery. A weaker spiral is present on the upper base in most specimens, below which the axial ribs disappear. Two prominent spiral cords encircle the lower base. The aperture is simple, subcircular and lacks any channels or notches. The peristome is duplicated and there is a prominent varix on the outer lip. The inner lip is separated from the parietal wall by a narrow, deep channel. The shell is chocolate brown, fading to orange when dead. Some specimens have narrow, indistinct yellowish bands at the periphery, suture and upper base but these are usually only visible in fresh material.

Head-foot (Fig.2). The cephalic tentacles (t) are strap-shaped and oval in section with a narrow, longitudinal strip of actively-beating cilia ventrally. The rest of the tentacles are unciliated except for a few stiff 'setae' distally. The eyes lie a little above the tentacle bases on their outer sides in small bulges. They have a well-developed pigmented retina and a lens. The rather long snout (sn) is distally bilobed, non-ciliated and non-retractile.

The foot is simple, being slightly wider anteriorly and posteriorly than in the middle, rounded behind and with a more-or-less straight anterior edge with rounded outer ends. The anterior pedal mucous gland (pg) lies in the anterior third of the foot and is narrower and longer than usual in rissoaceans, occupying only about half the width. It opens dorsally beneath a very narrow dorsal flap, all that remains of the propodium (pp), and extends posteriorly as far back as the anterior edge of the pedal ganglia in retracted animals.

The sole is covered with a columnar epithelium of non-staining mucous cells with wedge-shaped ciliated cells between. Dorsally the foot is covered with a ciliated cuboidal epithelium.

The head-foot is translucent white, except for the

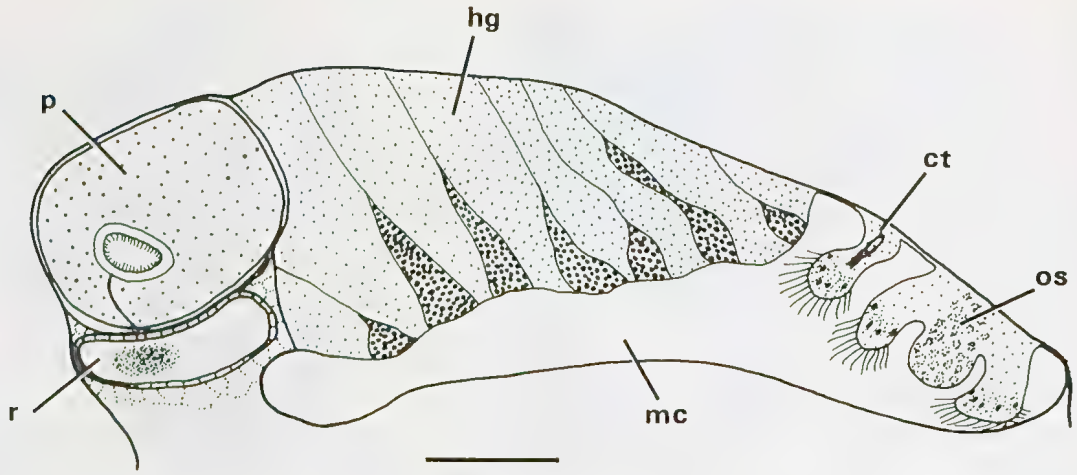

Fig. 3. A section through the pallial cavity of a male. **ct,** ctenidial filament; **hg,** hypobranchial gland; **mc,** mantle cavity; **os,** osphradium; **p,** penis; **r,** rectum. **Scale:** 0.05mm.

more opaque-white pedal gland and a small, triangular dense white patch behind the black eyes. Some specimens have a grey smudge on the narrow opercular lobes.

The operculum (Fig. 1C,D) is white in the living animal, transparent yellow when removed. It is thin, flat and lacks any projections on the inner surface except for a low ridge just inside the columellar edge and along the outer edge of the elongately oval muscle scar. The nucleus is eccentric and the last whorl is very large. In section it can be seen to be composed of two layers but these are not as clearly differentiated as they are in the Anabathrinae (Ponder, 1985).

Pallial cavity (Fig. 3). The osphradium (os) is large and conspicuous, occupying the left side of the pallial cavity. It consists of an unciliated, elongately oval sensory central area containing the osphradial ganglion which is surrounded by a ciliated ridge. A few (at least five) short, finger-shaped ctenidial filaments (ct) lie in the posterior end of the pallial cavity, near the posterior end of the osphradium. These are ciliated and contain skeletal rods. A massive hypobranchial gland (hg) occupies much of the cavity. Large, colourless cells, up to 0.13 mm in length, make up the bulk of the gland and wedge-shaped, dark red-staining cells lie distally. In males, the penis (p) is folded backwards into a sheath behind this gland.

Alimentary canal (Figs 4,5). The mouth is a ventral, longitudinal slit which opens to a spacious oral tube lined dorsally with a cuboidal, ciliated epithelium and with a pair of large folds ventrally. These folds are composed of a ciliated columnar epithelium which contains many mucous and red-staining gland cells. The salivary glands open from these folds opposite the anterior end of the odontophore. Behind this point the salivary glands lie within the folds (Fig.4, sg) and are thus latero-ventral to the buccal cavity. There are no jaws. The odontophoral cartilages (Fig. 4, od) are weakly developed and only a thin sheath of muscle surrounds them. The entire odontophore is only about half the width of the buccal mass.

The radula (Figs 1B, 2D) is small relative to the size of the animal, compared with other members of the superfamily, being only about 0.07 mm in length and 0.012 mm wide. It is particularly unusual in being triseriate. The squarish central teeth have a straight cutting edge with about seven small, equal-sized cusps on either side of a smaller median cusp. There are no basal processes but a prominent V-shaped projection lies on the inner face of each tooth and extends to the straight ventral margin. The subrectangular lateral teeth are about the same size as the central teeth. They have an almost straight cutting edge which extends over the whole length of each tooth and bears about 15 small, approximately equal-sized, sharp cusps. Each tooth has a thick, pillar-like supporting structure in the middle of the face which extends from just below the cutting edge to the ventral edge.

The short, tubular salivary glands contain only a single, pale-staining type of gland cell, and lie anterior to the cerebral ganglia. They disappear, along with the ventral folds, a little behind the odontophore. The posterior buccal cavity then becomes oval and can be regarded as the anterior oesophagus. It is lined with an irregular, ciliated epithelium in which are embedded many goblet cells. There is little clear distinction between the anterior oesophagus and posterior buccal cavity in size or in histology. As it passes through the nerve ring it is only slightly constricted. There is an ill-defined pair of low ventral folds and a very small mid-dorsal cleft is probably the food groove. The oesophagus appears to rotate as it passes through the nerve ring but the epithelium becomes very irregular behind the ring and any identifiable structures are lost. This epithelium consists of ciliated cells that range from very small cuboidal to elongate, finger-shaped cells that protrude from the epithelium. All of these cells have a similar simple cytoplasm, there being no gland cells present.

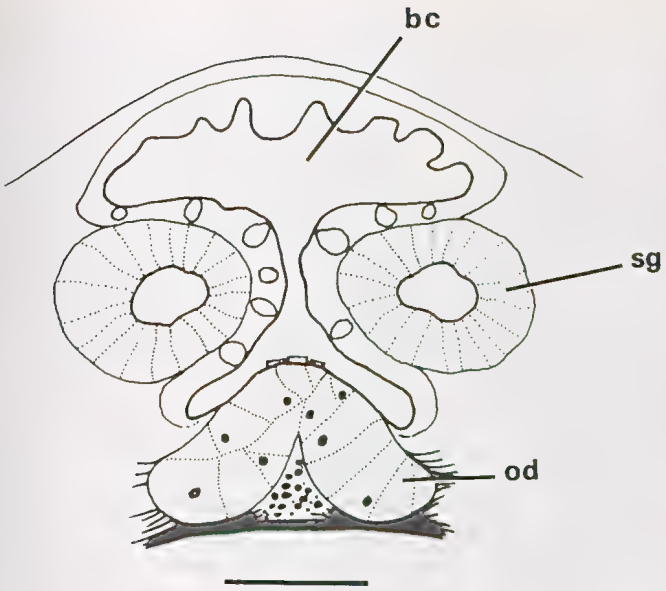

Fig. 4. A transverse section of the buccal mass. **bc**, buccal cavity; **od**, odontophoral cartilage; **sg**, salivary gland. **Scale:** 0.05mm.

The short posterior oesophagus has a simple, ciliated epithelium. There are no obvious muscle fibres in the wall of any part of the oesophagus.

The large stomach (Fig. 5) is about 0.5–0.6 mm in length and occupies the width of the visceral coil. It is divided into three parts, large posterior (pc) and anterior chambers (ac) and a very small style sac (ss). The posterior chamber is approximately circular in section and slightly longer than wide. It is lined with an irregular, approximately cuboidal, epithelium with very finely granular, pale-staining cytoplasm which contains large, clear vacuoles and irregularly placed nuclei. This chamber opens to the anterior chamber via an opening smaller than the diameter of the stomach, resulting in the two chambers being separated by a circular ridge of tissue. The lining of the anterior chamber is more typical of the gastric epithelium found in other prosobranchs. It is composed of a more regular epithelium in which the cells are, in places, elongated to form ridges/typhlosoles. Parts of this epithelium are ciliated, but most of it is not. The style sac lies at the anterior end of the stomach and is only about 0.09 mm in length. It is a small pocket lined with small cuboidal

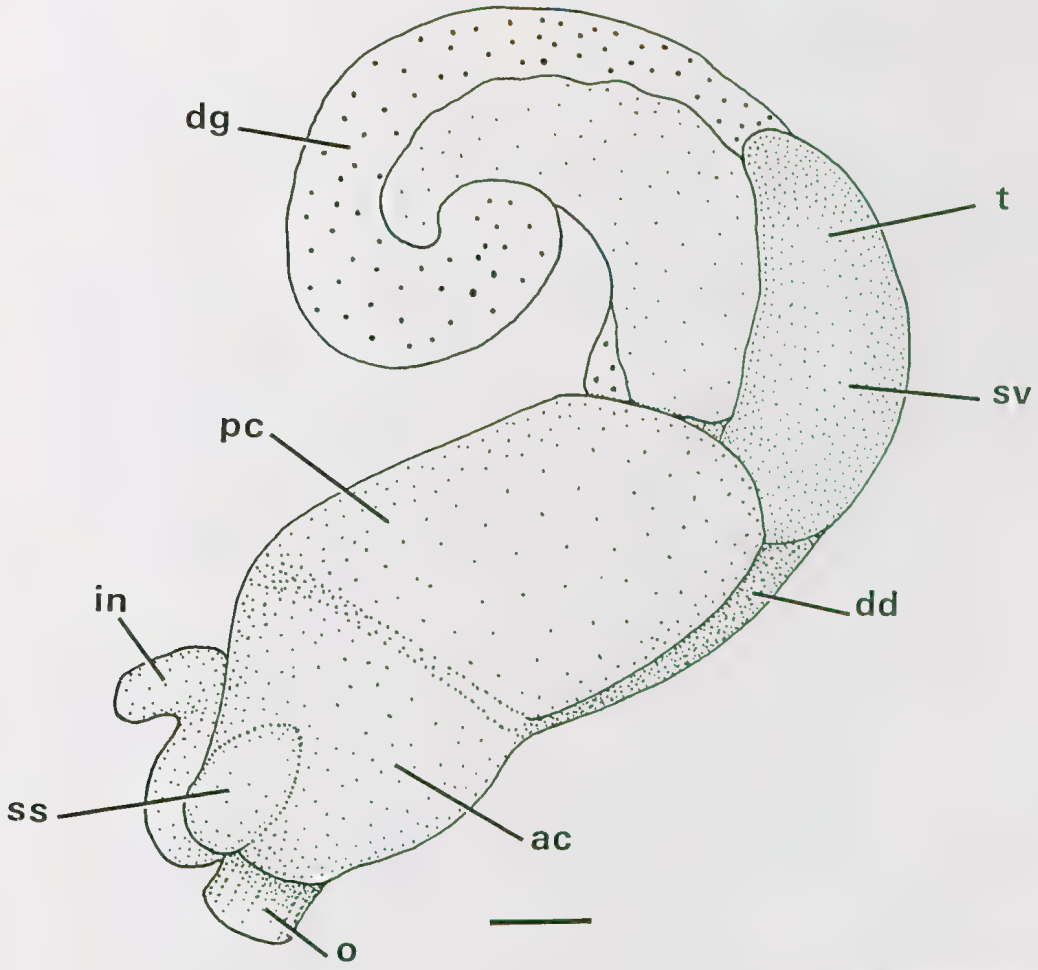

Fig. 5. The stomach and visceral coil of a male. **ac**, anterior chamber of stomach; **dd**, digestive gland duct; **dg**, digestive gland; **in**, intestine; **o**, oesophagus; **pc**, posterior chamber of stomach; **ss**, style sac; **sv**, seminal vesicle; **t**, testis. **Scale:** 0.1mm.

cells supporting conspicuous, short cilia, as is typical of the epithelium of this structure in many mesogastropods. An oval hyaline secretion lies within the style sac which may be a tiny crystalline style. The intestine opens to the proximal end of the sac, the distal end being a very short, separate bud. All of the gastric epithelium contains small numbers of tiny, dark, refringent granules. The oesophagus opens adjacent to the style sac and the long, narrow digestive gland duct (dd) opens at the junction of the two chambers.

The cytoplasm of spirally coiled foraminiferans, their tests dissolved either by the fixative or by digestive secretions, lie in both chambers and were present in all the specimens sectioned. They are up to about 0.25 mm in diameter and exist in all stages of digestion, some looking like large, ovoid amoebocytes. No other food particles are present in the stomach.

The posterior part of the posterior chamber lies alongside the anterior end of the single digestive gland tubule (dg) which forms the visceral coil, together with the gonad, behind the stomach. The digestive gland epithelium is composed mainly of columnar digestive cells up to about 0.04 mm in length, but small, triangular secretory cells, some containing dark brown spherules, are also present.

The intestine (in) is a simple tube that, after emerging from the style sac, bends at right angles to pass through the kidney parallel to the posterior end of the pallial cavity, and then enters the right pallial roof. It is lined with rather loosely packed, cuboidal cells with large vacuoles and non-staining cytoplasm that contains small numbers of refringent granules similar to those in the gastric epithelium. The intestinal epithelium adjacent to the style sac consists of larger, more irregular cells than the rest of the intestine, giving this initial section a spongy appearance in sections. The ciliated epithelium of the rectum consists of slightly smaller cells than those of the intestine, which may be cuboidal or pavement, depending on the amount of expansion of the lumen, and contain small, black pigment granules. The rectum (Fig. 3, r) forms a convoluted knot in the posterior corner of the pallial roof, the remainder undulating along the right side of the pallial roof to open well inside the pallial edge. It contains loose faecal pellets consisting mainly of minute brown to yellow granules and very occasional minute sand grains, etc. It is possible that calcareous material from the foram shells is also present in the faeces but this, like the foram tests in the stomach, would have been dissolved by the fixative.

Reproductive system. MALE: The testis (Fig. 5,t) consists of a single tubule which lies along the digestive gland and occupies nearly a whorl of the visceral coil, being about 0.43 mm in length. The testis opening is at its anterior edge where it opens to the seminal vesicle. The most conspicuous part of the seminal vesicle is a large diverticulum (sv) which lies on the outside of the testis/digestive gland, and extends behind the anterior edge of the testis for about 0.27–0.29 mm. Anteriorly the seminal vesicle continues behind the stomach as a swollen, sperm-filled tube which is about as long as the diverticulum. It then narrows to form the renal part of the vas deferens which is lined with ciliated, cuboidal cells containing black pigment granules, and enters the prostate gland just behind the posterior pallial wall. There are both typical and atypical sperm present, the atypical sperm being spherical and somewhat similar to those described in *Barleeia* (Slavoshevskaya, 1976).

The prostate gland is composed of pale, blue-staining columnar cells amongst which are scattered a few cells with red-staining granular contents. The prostate is circular in section and is embedded in the posterior-most part of the junction of the pallial roof and floor. It opens to a sperm groove in the posterior part of the pallial cavity which lies in the crease between the floor and roof of the pallial cavity. This groove passes up the neck, where its sides are raised and stronger cilia are developed, to the base of the penis. It then enters the penis where it becomes a closed penial duct. A line of fusion is, however, visible between the duct and the external epithelium.

The penis (Figs 2C; 3, p) is attached behind the right eye by a narrow base. It is as long as the pallial cavity (about 0.7 mm), approximately parallel-sided over the majority of its length, and tapers distally to a point. Almost the entire penis is enclosed in a sheath behind the hypobranchial gland (Fig. 3), with an opening on the anterior edge of the gland, and that extends to the posterior end of the pallial cavity.

FEMALE: The large, yolky eggs are up to about 0.18 mm in diameter in the only mature female sectioned. The ovary appears to consist of a single tubule and is probably shorter than the testis. The sections of this specimen are, unfortunately, not a complete series so that the description of this system is incomplete. There is a coiling upper glandular oviduct (Fig. 6, uog) composed of cells with orange-staining, granular contents. This probably opens to the blue-staining albumen gland (ag) (this connection was not actually observed because of missing sections) which, in turn, is continuous with the capsule gland (cg). This gland is composed of two sections, a posterior, mostly red-staining gland, a middle, thin-walled section and an anterior vestibule lined with goblet and ciliated cells. Most of the albumen gland and all of the capsule gland lie in the right side of the pallial roof. This pallial part of the oviduct appears to open to the pallial cavity by a terminal opening. Two immature females have most of the pallial oviduct open ventrally to the pallial cavity. No seminal receptacle or bursa copulatrix were observed but the absense of these structures is by no means certain.

Reno-pericardial system. The small kidney lies across the posterior end of the pallial cavity immediately anterior to the anterior wall of the stomach. It opens to the pallial cavity by way of a small pore that lacks any noticeable modification. A conspicuous renal gland on the outside wall of the kidney stains orange in Mallory's triple stain. The remainder of the epithelium

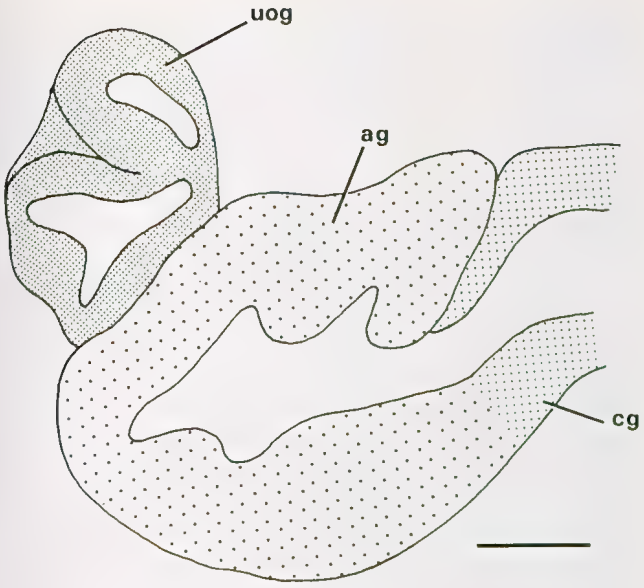

Fig. 6. Section through the upper part of the glandular oviduct. **ag**, albumen gland; **cg**, capsule gland; **uog**, upper oviduct gland. **Scale:** 0.05mm.

consists of a single layer of cells.

The small pericardium contains a typical mesogastropod heart which lies immediately behind the posterior-most ctenidial filament. A portion of the common wall between the pericardium and the kidney is very thin in both sexes, but there is no reno-pericardial duct.

Nervous system. The circum-oesophageal ganglia lie immediately behind, and partly overlie, the buccal mass. They form a concentrated ring with a very short connective (virtually abutting) between the cerebro-pleural and pedal ganglia; the cerebral ganglia abut one another as do the pedal ganglia. The oval pedal ganglia are about the same size as the cerebral ganglia and lie immediately anterior to them. They have a large (about half the length of the pedal ganglion) pair of statocysts, each containing a single statolith, partially embedded posteriorly. The pleural ganglia are markedly smaller than the cerebral ganglia (approx. ¼ of the size) to which they are fused. The suboesophageal ganglion lies immediately behind the statocyst attached to the left pedal ganglion and is about half the length of the cerebral ganglia. It is attached to the left pleural ganglion by a very short connective, so that it is virtually abutting. The supraoesophageal ganglion is about half the size of the suboesophageal ganglion and is attached by a short connective, about the same length as the ganglion.

Discussion

The main characters separating *Emblanda* from the subfamilies of the Barleeidae and the families judged to be most similar to the Barleeidae (although not necessarily closely related), are listed in Table 1. These families, the Barleeidae, Cingulopsidae, Eatoniellidae and Rissoidae, have been the subject of recent revisions and the family characters and limits are well established.

Table 1 shows that, of the characters listed, four are unique to *Emblanda* when compared with the Barleeidae (by combining the data for the two subfamilies Barleeinae and Anabathrinae). These are the triseriate radula, the narrow digestive gland duct, the penial sheath behind the hypobranchial gland and the glandular upper oviduct. This latter character alone excludes *Emblanda* from the Barleeidae, all barleeids having a simple, narrow oviduct behind the albumen gland (Ponder, 1984). It is unfortunate, however, that more details of the female genital system are not known as it seems likely that additional differences may exist.

The Rissoidae, differs in five characters. The shell of *Emblanda* resembles the rissoid genus *Merelina* and the glandular upper oviduct is an important shared character. There are, however, significant differences, apart from the penial sheath and the radula. No rissoid has an inner chitinous shell layer, a double-layered operculum or lacks jaws. Most have pallial and/or metapodial tentacles and all have a multitubular digestive gland with a wide opening to the stomach, including those that feed on forams. The Cingulopsidae and Eatoniellidae differ in 12 and 15 characters respectively.

A new suprageneric taxon appears to be justified because of the unique combination of characters, the most remarkable being the very unusual radula. There are very few examples in the Taenioglossa in which the radula is considerably modified. The conservative nature of this structure in the group is in marked contrast to the plasticity that can be observed in the Neogastropoda (Ponder, 1973) and in the Archaeogastropoda (e.g. Hickman, 1983). Warén (pers. comm.) has found considerable plasticity in the radulae of some cerithiaceans but the vast majority of this group have a normal taenioglossan radula.

The radula alone is, against this background, probably sufficient reason for giving *Emblanda* higher category status. The anatomical studies have provided strong additional evidence to support the erection of a new suprageneric taxon.

There are only a few characters known to separate *Emblanda* from the Barleeidae. Three of these are, however, judged to be of considerable importance. The glandular upper oviduct is a character that alone should exclude *Emblanda* from the Barleeidae; a similar, but probably convergent, structure occurs in the Rissoidae. A triseriate radula is known in only one other possible mesogastropod, *Turritellopsis* (Turritellidae? or possibly Mathildidae)(Sars, 1878). This genus is not, in any other way, similar to *Emblanda*. The penial sheath behind the hypobranchial gland does not appear to have been described in any other gastropod.

The evidence suggests that *Emblanda* may be derived from a barleeid ancestor but has diverged by acquiring a number of specialized characters. Some of these, the

Table 1. Comparison of selected characters of *Emblanda* with the families judged to be most similar.

	Emblandidae	Barleeinae	Anabathrinae	Cingulopsinae	Eatoniellidae	Rissoidae
Protoconch	2	2	2	1	1	1(2)
Inner chitinous Layer	1	1	1	1	1	2
Operculum	2	1	2(1)	1	1	1,2
Cephalic tentacles	2	1	3	1,2	1	2
Pallial tentacles	2	2(1)	2	2	2(1)	1,2
Metapodial tentacles	[1]	2(1)	2	2	2	1,2
Opercular lobe tentacles	2	2	2	2	1,2	2
Posterior pedal gland	2	1a	1a,2	1a	1a	1b,2
Radula	2	1	1	1	1	1
Jaws	2	1,2	1,2	2	1	1
Salivary glands	2	2	2	1	1	2
Oesophagus	2	2(1)	2	1	1	2
Stomach	2	2	2	1	1	2
Digestive gland duct	2	1	1	1	1	1
Prostate gland	2	2(1)	2	2	1	2(1)
Pallial vas deferens	1	2(1)	2	2	1	2(1)
Penis	2b	2a	2a	1	1	2a
Upper oviduct gland	2	1	1	1	1	2
Pallial oviduct	2?	2	2	2	1	2(1)

Numbers enclosed in brackets are states rarely encountered, those enclosed in square brackets are weakly developed. The character states are arranged with that state judged to be the most primitive (within the families being considered) first. I have discussed in detail these characters and their states elsewhere (Ponder, 1984, 1985).

Character states used in Table 1 follows. Information is mostly from: Barleeidae (Ponder, 1984), Cingulopsidae (Fretter & Patil, 1958 and Ponder, 1968), Eatoniellidae (Ponder, 1968), Rissoidae (Ponder, 1985).

Protoconch: 1, smooth or with raised sculpture; 2, punctate. **Inner chitinous layer:** 1, present; 2, absent. **Operculum:** 1, with peg on inner surface; 2, lacking peg. **Cephalic tentacles:** 1, tapering; 2, parallel-sided; 3, paddle-shaped. **Pallial tentacle(s):** 1, present; 2, absent. **Metapodial tentacle(s):** 1, present; 2, absent. **Opercular lobe tentacle(s):** 1, present; 2, absent. **Posterior pedal gland:** 1, present; la, with groove to posterior end of foot; 1b, without groove to posterior end of foot; 2, absent. **Radula:** 1, taenioglossate; 2, triserial. **Jaws:** 1, present; 2, absent. **Salivary glands:** 1, glands or their ducts pass through nerve ring; 2, glands or their ducts do not pass through nerve ring. **Oesophagus:** 1, with oesophageal gland or pouches; 2, without gland or pouches. **Stomach:** 1, without crystalline style; 2, with crystalline style. **Digestive gland duct:** 1, wide opening to stomach; 2, long and narrow. **Prostate gland:** 1, open; 2 closed. **Penis:** 1, absent; 2, present; 2a, housed in mantle cavity; 2b, housed in sheath behind hypobranchial gland. **Upper oviduct gland:** 1, absent; 2, present. **Pallial oviduct:** 1, open along most of length; 2, terminal opening only.

features of the alimentary canal including, possibly, the radula, may be associated with feeding on foraminiferans. *Rissoina chathamensis* (Hutton) (Ponder, 1968) feeds on foraminiferans and, like *Emblanda*, has a long posterior chamber and a relatively small style sac. The rest of the alimentary canal, including the radula, is, however, like that of other Rissoidae. The characters of the reproductive system are clearly not related to the feeding specialization and provide important supporting evidence of the morphological separation of *Emblanda* from the Barleeidae.

A new family-level taxon within the Rissoacea appears to be justified and a new family Emblandidae is proposed and diagnosed below.

EMBLANDIDAE n.fam.

Diagnosis. *Shell.* Minute (up to about 2 mm in length), ovate-conic, solid, non-umbilicate, with axial and spiral ribs. Protoconch paucispiral, dome-shaped, first half whorl deviated, very minutely and irregularly pitted. Aperture subcircular (separated from parietal wall in only known species), peristome entire, duplicated, lacking distinct notches. Outer lip with varix.

Operculum. Oval, simple, thin, composed of two layers, with eccentric nucleus, last whorl large.

Radula. Triseriate, cusps small, equal-sized, numerous.

Head-foot. Cephalic tentacles long, parallel-sided, ciliated. Snout long, rather narrow, bilobed distally.

Foot simple, with approximately straight anterior edge, rounded behind and with elongate, narrow anterior pedal gland opening beneath propodium. Propodium much narrower than anterior edge of foot and placed behind it. No pallial tentacles. Rudimentary metapodial tentacle.

Anatomy. Osphradium large, surrounded by cilated ridges; ctenidium vestigial to small. Hypobranchial gland massive, occupying most of pallial roof and with a sheath behind to accommodate penis in males.

Jaws absent, odontophore (and radula) much reduced, salivary glands paired, contained within ventro-lateral buccal folds and, therefore, terminate anterior to cerebral ganglia and never dorsal to posterior buccal mass. Anterior oesophagus about equal in width to buccal cavity, mid-oesophagus simple. Stomach with very small style sac (containing style) into which intestine opens; posterior chamber longer than anterior chamber and histologically distinct. Digestive gland a single tubule, opening to stomach at junction of anterior and posterior chambers by way of long, narrow duct.

Male with long penis attached to head behind right eye and held in sheath behind hypobranchial gland. Penial duct closed but pallial vas deferens an open, ciliated groove. Prostate gland small, closed, in posterior pallial wall. Seminal vesicle with diverticulum. Female with coiled glandular duct posterior to albumen gland. Albumen and capsule glands continuous, closed ventrally when mature, open when immature.

Genus *Emblanda* Iredale, 1955.

Type-species. *Rissoa emblematica* Hedley, 1906; original designation.

Diagnosis. As for family.

Emblanda emblematica (Hedley, 1906)

Rissoa emblematica Hedley, 1906:526, pl.32, fig.24 (type locality: Manly Beach, Sydney, New South Wales). —
Anabathron emblematicum.—Iredale, 1924:244; Cotton, 1944:312 (in part); Laseron, 1950:276, fig. 59.
Emblanda emblematica. — Iredale, 1955:81; Laseron, 1956: 445, fig.160.

Material examined. Holotype and 58 lots in the Australian Museum.

Distribution. Port Curtis, Queensland to Mallacoota, eastern Victoria. Found living in the lower littoral and shallow sublittoral zones amongst short algae.

Remarks. The shell of this species is very distinctive and there are no similar Australian species. Nor are any species known from other parts of the world that could be considered to be related. Virtually all of the available material on which the above records are based are empty shells. Such shells are rather rare in samples of 'shell sand' suggesting that the lack of success in finding numbers of this species alive may not be because the most favoured habitat has yet to be discovered.

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Avian Fossils from Quaternary Deposits in 'Green Waterhole Cave', South-eastern South Australia

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Abstract. Sixteen species of birds have been identified from Quaternary-aged deposits in 'Green Waterhole Cave' (L-81 of the Cave Exploration Group of South Australia cave classification) approximately twenty-four kilometres west of Mt Gambier, south-eastern South Australia. All but three species are referable to modern species. The exceptions are a new accipitrid (to be described by Drs P.V. Rich and G.F. van Tets), a new species of coucal, and a new species of passeriform. It is suggested that one of the extant species and all of the new taxa are examples of Pleistocene gigantism. Geographic range extensions are demonstrated for *Gallinula mortierii, Calyptorhynchus lathami* and the genera *Centropus* and *Orthonyx*. Taphonomic study of the deposit, using faunal composition as the main indicator, implies that water was the accumulating agent. Relative dating of the locality has been made by using sea level curves (last sea level transgression over the present eustatic high) and the presence of megafauna. Dating of the last sea level transgression suggests a maximum age of 125,000 years before present (y.B.P.) for the opening of the cave to the surface, because the cave lacks marine influence. The maximum age of accumulation is anytime before 15,000 y.B.P., which is the time of last occurrence of most mammalian megafauna.

Baird, R.F., 1985. Avian fossils from Quaternary deposits in 'Green Waterhole Cave', south-eastern South Australia. Records of the Australian Museum 37(6): 353–370.

Keywords: avian palaeontology, Quaternary, Green Waterhole Cave, South Australia, *Centropus, Orthonyx*, taphonomy.

'Green Waterhole Cave' (L-81 of the Cave Exploration Group of South Australia cave classification) is a drowned cave in the Tantanoola district of south-eastern South Australia, about twenty-four kilometres west of Mount Gambier (Fig. 1). The host rock is the Gambier Limestone of the Oligo-Miocene-aged Glenelg Group. L-81 lies on the border of the Kongorong Shank and Mt Gambier sections of Marker (1975). Karst production in this area, according to Marker, "has been promoted by late Quaternary marine fluctuations...". The cave shows no marine influence. The last marine incursion into the area at 124,000 y.B.P., therefore, may be taken as a maximum age for the opening of the cave (Shackleton & Opdyke, 1973; Bloom *et al.*, 1974). Karst development would have been aided by subsequent marine fluctuations, increased rainfall and greater seasonal temperature variations, especially during the last glacial (Sweeting, 1973: 156–157), therefore making it likely that the cavern opened to the surface sometime after the last interglacial.

The cavern probably opened in the latter half of the last glacial, based on the large proportion of extant species in the fossil avifauna. The floral history should give an idea of environmental changes during that time. The floral history of south-eastern South Australia and western Victoria is deduced from work on pollen-bearing sediments covering the past 50,000 y.B.P. collected within Lake Leake, S.A. and Lake Keilambete, Vic. (Dodson, 1974a, b, 1975). Briefly, the area was dominated by *Eucalyptus* woodland and heath before the oldest date of 50,000 y.B.P. (the limit of radiocarbon dating) up to 39,000 y.B.P. At this time, there was an ephemeral change to open formation that suggested dryer times. The flora reverted back to *Eucalyptus* woodland and heath understory at 38,000 y.B.P. After 35,000 y.B.P. the precipitation decreased. At about the same time, the coastline migrated further south as a result of the lowering of sea level synchronous with the last glaciation. It is assumed that, from then on, the area was drier than it had been at any other time in the last 50,000 years. *Casuarina* pollen, with

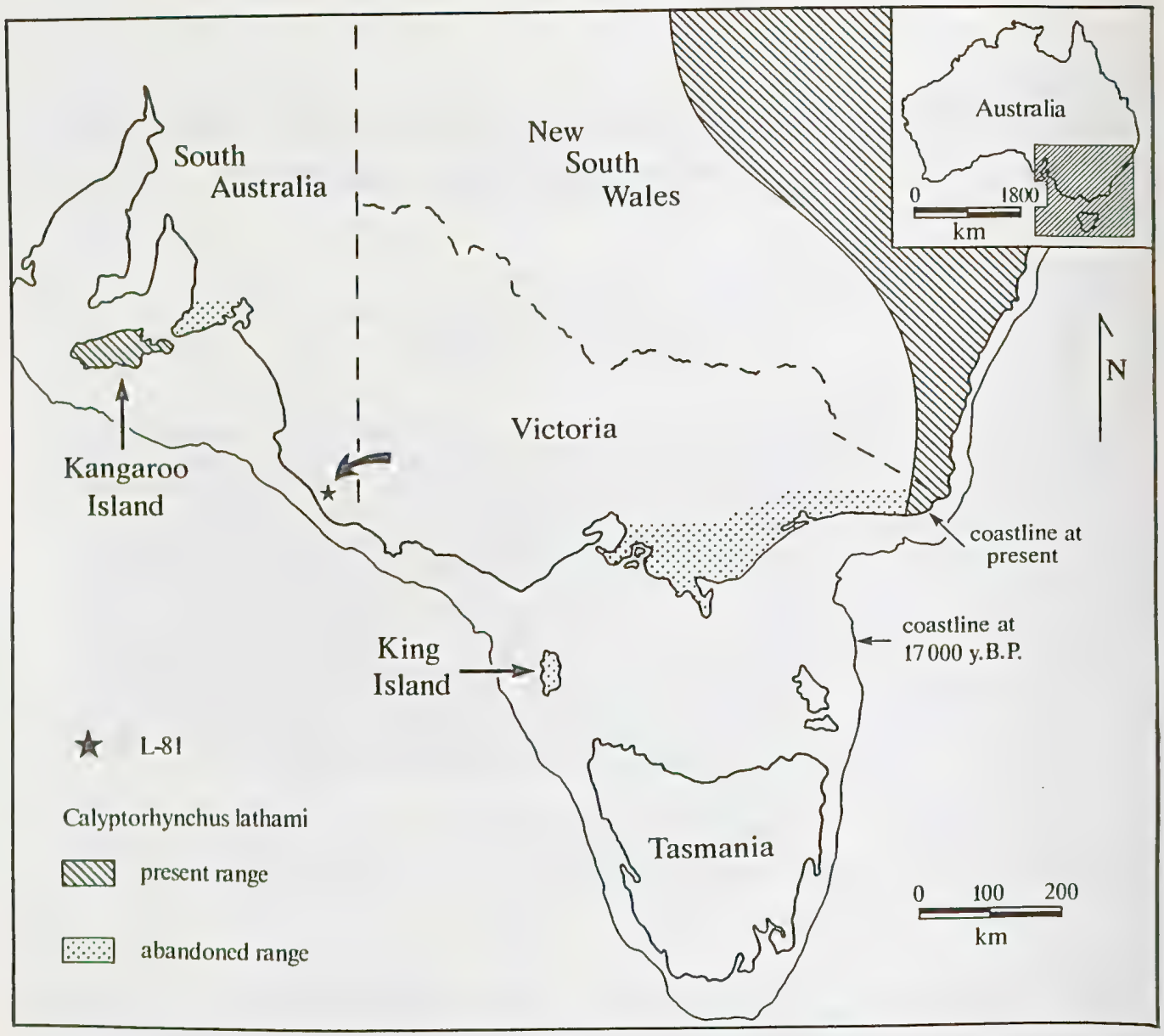

Fig. 1. Distribution of *Calyptorhynchus lathami* in south-eastern Australia including fossil locality, historical geographic range and present day geographic range.

diameters equal to or less than 24μm, dominates the microfloral assemblages continually from this time until approximately 10,000 y.B.P., when *Casuarina* greater than 28μm becomes dominant and continues so until the advent of European settlement. The *Casuarina* species with pollen diameters greater than 28μm is most likely to be *C. stricta*, due to its propensity to forming dense stands, therefore allowing its pollen to dominate microfloral assemblages, and its affinity to coastal and subcoastal areas (Kershaw, pers. comm.). Dodson suggested that, between 6,900 and 5,000 y.B.P., the area between Melbourne and Adelaide was wetter than the same area today, coinciding with the return of sea level to its current position (Thom & Chappell, 1975). The same scenario was suggested for the vegetation of the Nullarbor Plain where, during sea level regression, the vegetation would have changed from eucalypt scrub to treeless plain. Upon sea level transgression, the eucalypts became locally dominant once again (Martin, 1973). This sequence of events corresponds to the movement of the humid zone associated with the coastline. Since European settlement, most of the forest cover has been removed, a process advanced even by 1915 (Marker, 1975).

The dimensions and early history of excavation of 'Green Waterhole Cave' are described and figured by Pledge (1980). Additional material has since been collected under the supervision of Dr R. Wells in a series of trips between 19 January 1979 and 6 March 1979. Large amounts of postcranial material have been retrieved by Dr Wells, and the bulk of the avian material, here discussed, has come from his excavations.

Pledge found the mammalian assemblage to be of mixed age, with both extant and extinct taxa represented in a deposit which had lent itself to the mixing of noncontemporaneous material. Though there is a definite stratification to deposits at this site, interpretation is difficult due to post-depositional slumping of the talus cone and the constraints of underwater excavating (Wells, pers. comm.). The mode of accumulation, as hypothesized by Pledge, was through drowning and subsequent settling of the corpses. Hypotheses concerning the cause for the initial drowning vary, and in this paper another scenario is offered.

Prior lists of the avian species in 'Green Waterhole Cave' were correct in most of their higher taxa determinations. Incorrectly identified were the specimens referred to *Genyornis* and *Dromaius* mentioned in Williams (1980) and Rich & van Tets (1982), respectively. Both records are most probably referable to a single specimen of a juvenile macropod right femur. The *Megapodius* of Rich & van Tets (1982) was also misidentified and is, in actual fact, *Gallinula mortierii*.

ACCOUNT OF SPECIES

The scientific names used in each account follow Condon (1975) and Schodde (1975), except in the case of the fossil taxa, where I follow Brodkorb (1971). Taxa previously unknown from subfossil and fossil deposits are also noted. Inclusions in the faunal lists of Rich & van Tets (1982) are not considered to be 'formally confirmed records' as no full diagnoses were put forward. Minimum numbers of individuals were determined by the standard method of counting the most abundant element from a particular side.

Geographic ranges given for each extant species are from Wheeler (1967), Condon (1969), Green (1977), Parker & Reid (1983) and Blakers *et al.* (1984) and are here assumed to be the same as the present range, unless otherwise noted.

Specimens and specimen numbers belong to the South Australian Museum.

All measurements in the text are in millimetres (mm). Standard measurements are indicated in brackets and follow the guidelines in von den Driesch (1976). All measurements were taken with vernier calipers accurate to 0.05 mm and were rounded to the nearest 0.1 mm.

ACCIPITRIFORMES

Accipitridae

new species

Material. Complete left and right ulnae (P.24324 & 24323), complete left and right radii (P.24325 & 24326), complete left and right carpometacarpi (P.24327 & 24328), all from site 07. In addition, there is a fourth thoracic vertebra (P.24329), site unknown, which seems referable to this taxon. The specimens represent a minimum of 1 individual.

Remarks. This form will be fully described at a later date by Drs P.V. Rich and G. van Tets.

Interestingly, the left and right radii are completely different in colour, one being dark brown and the other being light tan. In all other respects the elements seem to be identical. This should be kept in mind when other composite skeletons from the deposit are being considered for it suggests that the coloration of each element may not be a reflection of its relative time of deposition.

Falconidae

Falco cf. *berigora*

Material. Incomplete right femur (P.24330).

Remarks. The specimen is assigned to this species on the basis of overall length measurement and slenderness. As compared with other Australian falconids of similar size (*F. peregrinus* and *F. subniger*), *F. berigora* has the most slender limb elements (Rich, van Tets & McEvey, 1982). Usually slenderness in postcranial elements varies concurrently with overall size and would not be a reliable character to base species identification on. But because *F. berigora* is unusual in that it is so consistently gracile through its size range, I have referred the element to this species.

GRUIFORMES

Rallidae

Gallinula mortierii

Material. Complete (P.24236) and incomplete (P.24237) right femora, incomplete left tibiotarsus (P.24238), proximal end of a left tibiotarsus (P.24234), 3 complete right tibiotarsi (P.22951, 24232 & 24233), incomplete right tibiotarsus (P.24239), incomplete left fibula (P.24235), and first phalanx for digit II (P.17349). The 10 specimens represent a minimum of 4 individuals.

Remarks. The main diagnostic features used in the identification of *Gallinula mortierii* are the large size and stoutness of its postcranial elements, whose dimensions are greater than those of all other Australian rallids (Olson, 1975). Measurements of *G. mortierii* material from Late Pleistocene-aged deposits are presented in Baird (1984).

The continental Pleistocene distribution for *G. mortierii* ranged from Kangaroo Island to Queensland. The largest concentration of fossil sites containing this species are centred about the Glenelg River region (Baird, 1984). The material from L-81 included the smallest tibiotarsus from any site in continental Australia, but its measurements could not be included in the statistics of Baird (1984) due to its incompleteness. Several of the *G. mortierii* elements from L-81 were larger than average, so a normal size distribution can be assumed for the fossil population from this site. The species is currently restricted to the island of Tasmania.

COLUMBIFORMES

Columbidae

Phaps chalcoptera

Material. Two incomplete left tibiotarsi (P.24331 & 24332).

Remarks. Three species of large columbid currently occur in south-eastern South Australia, *Phaps chalcoptera, P. elegans* and *Ocyphaps lophotes*. *Ocyphaps lophotes* is considered to be a relatively recent immigrant to the south-east, having colonized within the last 30 years (Parker & Reid, 1983). These three species exhibit considerable overlap in tibiotarsal lengths. The smallest and largest species can be identified beyond the areas of overlap with some certainty, but the median species cannot, on length measurements alone (see Table 1). The lengths of the fossil specimens (P.24331 & 24332) are 51.0 mm and 55.0 mm, respectively. Although the larger specimen may be reasonably referred to *P. chalcoptera*, the smaller is essentially indeterminate by size and, therefore, can only be referred to *Phaps* sp.

Table 1. Tibiotarsi length measurements [La] of the large columbid species presently inhabiting the area around L-81, south-eastern South Australia.

	mean	S.D.	min	max	N
Phaps chalcoptera	54.2	1.8	51.0	56.3	10
P. elegans	51.0	1.6	47.8	53.1	10
Ocyphaps lophotes	46.6	2.0	43.9	49.5	10

PSITTACIFORMES

Cacatuidae

Calyptorhynchus magnificus

Materials. Incomplete cranium (P.24333), incomplete left humerus (P.24335), distal end of a right radius (P.24336) and complete right femur (P.24337). The 4 specimens represent a minimum of 1 individual. Neither the genus nor species have been recorded previously in the fossil record.

Remarks. Characters distinguishing *Calyptorhynchus* from the larger species of *Cacatua* are listed in Table 2. Most apparent are the differences in the crania, with the crania of calyptorhynchids being anteroposteriorly elongate and dorsoventrally flattened. The cranial lengths and widths vary greatly among species in *Calyptorhynchus*, and the incomplete cranium (P.24333) falls well within the range of *C. magnificus* (Fig. 2). The cranium of *Callocephalon* exhibits features similar to those seen in *Calyptorhynchus*, although such modifications are probably correlated with feeding mechanics. Because of the convergent characters in the skulls of *Callocephalon* and *Calyptorhynchus*, postcranial characters, rather than cranial characters, appear to be more reliable for generic level identification because of their uniformity within each genus. This is due to the fact that feeding mechanisms may exhibit considerable plasticity intragenerically in the Cacatuidae, while locomotor mechanisms within generic groups remain essentially unvaried. Therefore, at the species level, both cranial and postcranial elements are useful for identification but, at the generic level, postcranial elements are more reliable due to their intrageneric uniformity. *Calyptorhynchus magnificus, C. funereus* and *C. lathami* differ considerably in size (see Appendix), and the fossil humerus (GL = 80.6) and femur (GL = 58.1) fall only within the size ranges of these elements for *C. magnificus*.

Calyptorhynchus lathami

Material. Incomplete rostrum (P.24334). Species previously unrecorded in the fossil record.

Remarks. Identification of *Calyptorhynchus* species can be easily accomplished using characters of the rostrum (Fig. 3). In *C. lathami*, the rostrum is anteroposteriorally short, laterally broad, with a diagnostic swollen dorsal surface and external nares that are level with the surface. In *C. funereus*, the rostrum is anteroposteriorly long, laterally flattened and with external nares that are level with the surface. In *C. magnificus*, the anteroposterior length of the rostrum is intermediate between that of *C. funereus* and *C.*

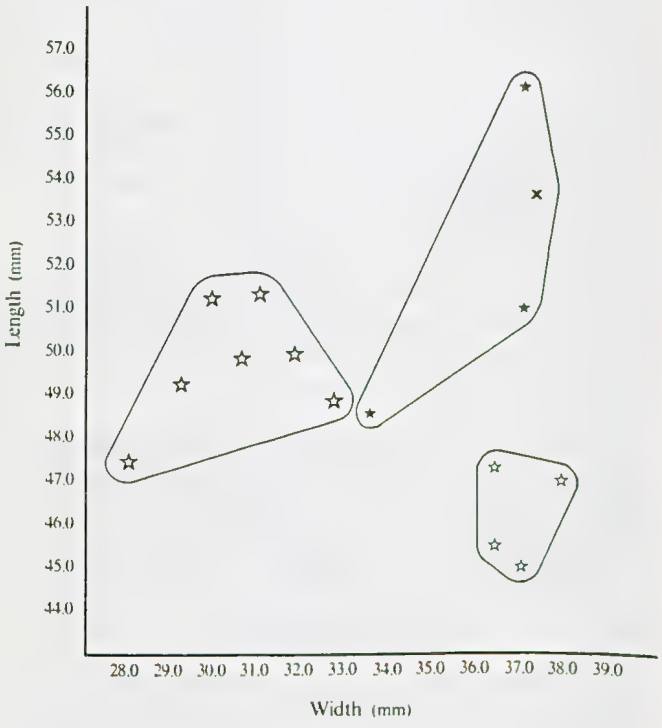

Fig. 2. Plot of cranial measurements (length [LP] and width [SBO]) of extant species in the genus *Calyptorhynchus*, including *C. lathami* (small open stars), *C. funereus* (large open stars) and *C. magnificus* (small closed stars). The X denotes the position of the fossil cranium (P.24333) on the plot.

Table 2. Morphological characters separating *Calyptorhynchus* from all other Australian cacatuids.

	Calyptorhynchus	Other cacatuids
Rostrum		
• external nares	• very small	• very large
Cranium		
• temporal foramen	• very large	• small
• temporal fossa	• proximodistally and dorsolaterally expanded	• proximodistally short and dorsolaterally narrow
• occiput	• displaced distally (not beneath the braincase)	• positioned beneath braincase
• tympanic wing of the exoccipital	• occupies a vertical plane	• occupies a horizontal plane
Humerus		
• bicipital crest	• gently slopes into shaft distally	• abruptly joins shaft distally
• pneumatic fossa	• shallow	• deep
• angle between the shaft axis and capital groove axis	• small	• large
• ventral tubercle	• proximodistally facing	• ventrally facing
Coracoid		
• brachial tuberosity	• extends further humerally	• extends humerally to a lesser degree
• impressio M. sternocoracoidius	• is more elongate humerosternally	• is less elongate humerosternally
Femur		
• fossa just below the antitrochanter articular facies on ventral side	• shallow	• deep
Tarsometatarsus		
• sulcus on the trochlea for digit three	• very shallow	• very deep

lathami. *Calyptorhynchus magnificus* also has a diagnostic ridge running dorsally between the two external nares, and external nares that are not level with the surface, but raised on small pedestals. Many workers have noted differences in the shape of the rhamphotheca in *C. magnificus, C. funereus* and *C. lathami* (Forshaw, 1969:51), but no-one has correlated these with equally large differences in the rostra. The form of the rhamphotheca depends upon the particular species' diet and can even vary between different populations of the same species. Ford (1980) demonstrated that the variation in the rhamphotheca in *C. magnificus* is correlated with the diet of the different populations. Populations in mid-western Western Australia have a large rhamphotheca and are ground feeders, concentrating on the large seeds of *Emex australis*. Populations in south-eastern South Australia and western Victoria have relatively small rhamphotheca and feed arboreally on seeds of *Eucalyptus baxteri* and *E. macrorhyncha*. Similar variability exists in south-western populations of *C. funereus sensu lato* (Saunders, 1974). Although the ramphethecae vary greatly between these populations, the rostra demonstrate less variability and are markedly constant within a species, while quite different between species.

Calyptorhynchus lathami, unlike its congeners, has a strong dependence upon seeds of one genus of plant throughout its range, *Casuarina* (including *Casuarina stricta, C. littoralis* and *C. torulosa;* Cleland & Sims, 1968). This relationship was first noted some time ago (North, 1896) and has been substantiated by recent studies of the species' ecology (Joseph, 1982). Of the species in the genus *Casuarina* with pollen diameters over 28μm (Kershaw, 1970), it is important to note that *C. stricta* is assumed to be the species of *Casuarina* dominating microfloral assemblages for the region from 10,000 y.B.P. to the present (Dodson 1974a, b, 1975; Kershaw, pers. comm.).

The range of *C. lathami* has contracted since European settlement of south-eastern Australia (North, 1896; Backhouse, 1843; Lendon, 1968). Given the geographical position of L-81 (see Fig. 1), the evidence strongly suggests that the species once had a continuous distribution at least as far west coastally as Kangaroo Island. Hypothetically, the last glacial lowering of the sea, which reached its lowest level around 15,000–18,000 y.B.P. (Martin & Peterson, 1978), would have allowed the range of *C. lathami* to be extended south and west of its present eastern limits, along the expanded coast and possibly onto the coastal plain exposed between Tasmania and the mainland. It is possible that the distribution from the east coast of Australia to Kangaroo Island could have been complete from as early as 18,000 y.B.P. As *Casuarina stricta* is a coastal species, the distribution of *Calyptorhynchus lathami* would have fluctuated back and forth with the changes of the coastline. This type of change would have left relict populations of *Calyptorhynchus lathami* on all those islands capable of supporting large stands of *C. stricta*. This hypothesis is to some extent corroborated by Green & McGarvie's (1971) report that *Calyptorhynchus lathami* may have occurred on King Island. It is proposed that the ultimate prehistoric distribution, which was presumably continuous to Kangaroo Island, was split by the sea level rising into the volcanic region of Victoria's western districts. The habitat on the volcanic plains, savannah grassland, is regulated not by precipitation but by the volcanic rock substrate, and hence tends to resist changes in the vegetation during climatic amelioration (Dodson, 1974a). This would have effectively fragmented *C. lathami*'s habitat, leaving disjunct distributions to the west and east. These populations have since been separated even further through land clearance

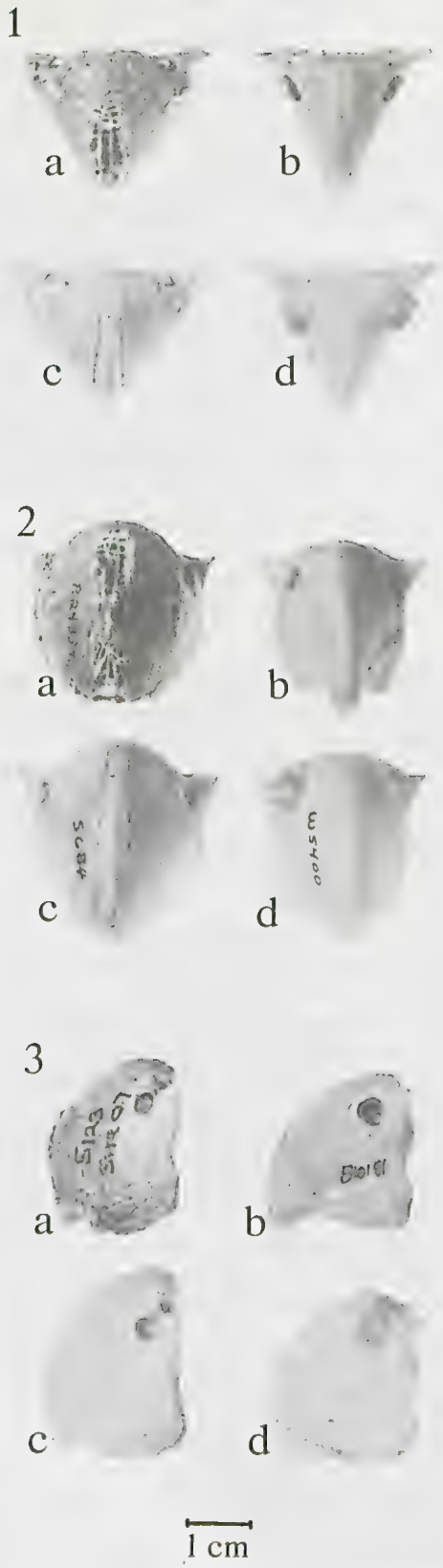

Fig. 3. Rostra of the three species of *Calyptorhynchus* inhabiting south-eastern Australia, *C. lathami* (AM S684) [1c, 2c, 3c], *C. funereus* (MV B10181) [1b, 2b, 3b], *C. magnificus* (MV W5400) [1d, 2d, 3d], compared with the fossil *Calyptorhynchus* rostrum (P.24334) [1a, 2a, 3a]: 1, dorsal views; 2, anterior views; 3, lateral views.

accompanying European settlement, eventually restricting the populations to the far east coast of the Australian mainland and to Kangaroo Island, South Australia.

Callocephalon fimbriatum

Material. Complete cranium (P.24338). Genus previously unrecorded in the fossil record.

Remarks. The skull of *Callocephalon*, with its less domed cranium (due to the distended occiput), large temporal fossa and diminutive size, is remarkably similar to the skulls of *Calyptorhynchus* spp.. Both are quite distinct from those of all other Australian cockatoos (see Appendix). An additional distinctive character in *Callocephalon* is the narrow bridge between the orbit and the anterior-most point of the cranium, as viewed laterally, which distinguishes this species from those of *Calyptorhynchus*.

Callocephalon fimbriatum was probably removed from its former range throughout the south-east of South Australia by the extensive land clearance during the initial stages of European settlement. At present, *C. fimbriatum* is quite abundant in the Lower Glenelg National Park along the Victorian and South Australian border and, given sufficient forest expansion, would probably frequent the south-east of South Australia (see Condon, 1969).

Cacatua tenuirostris

Material. Three incomplete crania (P.18301, 24339 & 24340), incomplete rostrum (P.24341), 11 complete or partial left humeri (P.18320, 24342–24351), 31 complete or partial left humeri (P.17287, 17311, 17322, 17323, 18334, 24352–24364), 10 complete or partial left ulnae (P.17332, 17333, 18340, 24365–24370), 11 complete or partial right ulnae (P.17324, 17325, 18340, 24371–24380), 3 incomplete left radii (P.24390–24392), 2 distal fragments of left radii (P.18318 & 18318), 7 complete right radii (P.24381–24389), 2 proximal fragments of right radii (P.24388 & 24389), distal end of a right radius (P.18318), 7 complete or partial left carpometacarpi (P.17336, 17337, 18321, 18338, 24393, 24394), 5 complete or partial right carpometacarpi (P.17327, 17342, 24395–24397), 3 complete right coracoids (P.17346 & 18336), 3 partial sterna (P.24398–24400), 7 complete or partial left femora (P.17329, 17339, 17340, 24401–24403), 3 complete or partial right femora (P.24404–24406), 5 complete or partial left tibiotarsi (P.17330, 24416–24419), 8 complete or partial right tibiotarsi (P.24407–24415), incomplete left tarsometatarsus (P.17344), 2 incomplete right tarsometatarsi (P.24420 & 24421) and incomplete synsacrum (P.17328). The 127 specimens represent a minimum of 31 individuals. Species previously unrecorded in the fossil record.

Remarks. *Cacatua* can be distinguished from *Calyptorhynchus* by the characters set out in Table 2. Therefore, the determination of *Cacatua tenuirostris* need involve only the genus *Callocephalon* and other species in the genus *Cacatua*.

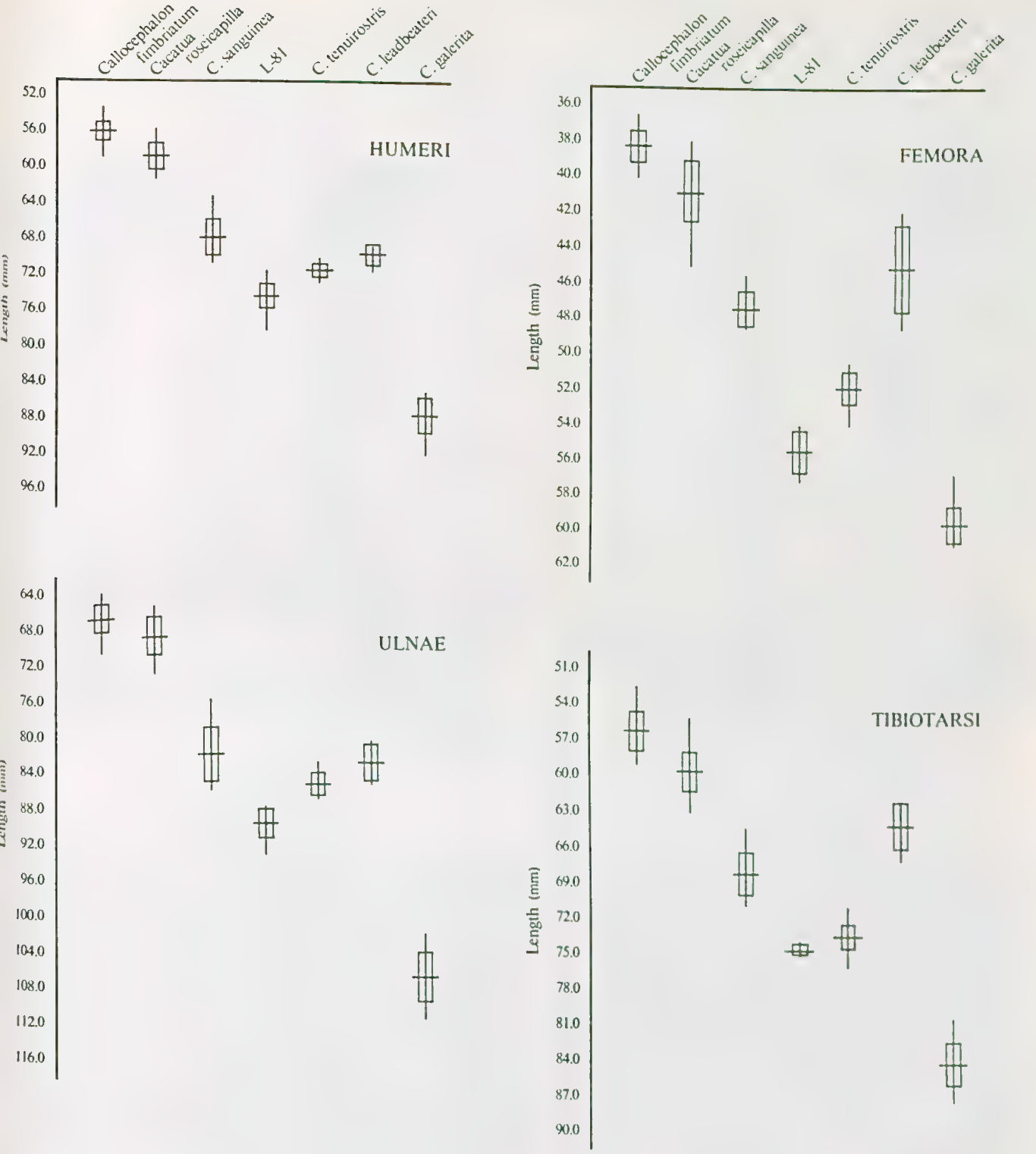

Fig. 4. Length measurements of humeri, ulnae, femora and tibiotarsi of *Cacatua* specimens from L-81 compared with those for all other south-eastern Australian representatives of the genera *Cacatua* and *Callocephalon*. Horizontal line is the mean, vertical the range and open box 90% of the population.

For conservation of space I will deal only with the most abundant element of *C. tenuirostris* in the deposit, the humerus: the distinguishing characteristics for all other elements can be seen in Figure 4. For the species of cockatoo involved, there can be designated three groups of humeral lengths, i.e., small, medium and large (see Fig. 4 and Appendix). The small-size group includes *Callocephalon fimbriatum* and *Cacatua roseicapilla*. Humeri of *C. fimbriatum* are most similar to calyptorhynchids in that the bicipital crest gently slopes into the shaft distally, the pectoral crest is positioned further distally than that of other cacatuids, and the pnuematic fossa is shallow. The humerus of *C. roseicapilla* differs from that of *C. tenuirostris* in having a small pneumatic fossa, and in its diminuitive size.

The large-size group consists of only *C. galerita*,

Table 3. Morphological characters separating the south-eastern populations of *C. tenuirostris* from *C. sanguinea* (for specific length measurements see Appendix).

	C. tenuirostris	*C. sanguinea*
Rostrum		
• diameter of external nares	• greater	• lesser
• width between external nares	• greater	• lesser
• culmen curvature	• lesser	• greater
• distinct tomial notch	• lacking	• present
Humerus		
• on the anterior face of the pectoral crest	• small posterior groove	• no groove
• pneumatic fossa	• deep	• shallow
• angle between the capital groove and the shaft axis	• greater	• lesser
Ulna		
• length	• greater	• lesser
Carpometacarpus		
• length	• greater	• lesser
Coracoid		
• length	• greater	• lesser
Femur		
• fossa just below the antitrochanter articular facies on the ventral side	• double	• single
Tibiotarsus		
• length	• greater	• lesser
Tarsometatarsus		
• length	• greater	• lesser

whose humerus differs from that of *C. tenuirostris* in having a less attenuate pectoral crest. Because of the lack of dorsal expansion, the pectoral crest slopes distally with a lesser angle into the shaft. The humeral shaft in *C. galerita* is also relatively stouter.

Of the medium-size group. *C. sanguinea* and *C. tenuirostris* differ from *C. leadbeateri* in their laterally expanded pectoral crests (*C. leadbeateri* is similar to *C. galerita*), and their prominant ventral midshaft ridge. This last feature is lacking in both *C. leadbeateri* and *C. galerita*. *Cacatua sanguinea* and *C. tenuirostris* can be separated by characters given in Table 3.

The fossil material conforms to all aforementioned characters of *Cacatua tenuirostris*, although, as can be seen in Figure 4, for the fossil elements considered, most are clearly larger than the sample population of *C. tenuirostris*. The average difference between the mean values of the fossil and modern populations is four percent. This is considered to constitute an avian example of Late Pleistocene gigantism similar to that seen in Victorian samples of the kangaroo species *Macropus giganteus* (Flannery, 1981). Therefore, the fossil material is here still considered referable to the extant species, *Cacatua tenuirostris*.

As with other large species in the order Psittaciformes, *Cacatua tenuirostris* has had a history of range contractions and expansions (Jarman, 1979). The species has been ubiquitous in south-eastern South Australia since European settlement (Parker & Reid, 1983).

Cacatuidae indeterminate

Material. Anterior cranial fragment (P.24422), 5 right humeral fragments (P.24423–24427), 2 left ulnal fragments (P.17331 & 17334), right ulnal fragment (P.17289), 4 left tibiotarsal fragments (P.24429–24432) and 5 right tibiotarsal fragments (P.17326, 24433–24436). The 18 specimens represent a minimum of 5 individuals.

Remarks. All of these specimens are deficient in the regions where diagnostic characters occur, but most are sufficiently intact to be placed within the Cacatuidae on morphology and size.

Platycercidae

Platycercus sp.

Material. Incomplete rostrum (P.17345). Family previously unrecorded in the fossil record.

Remarks. The specimen has a tomial notch and a width of 11.2 mm (measured ventrally at the midpoint between the external nares). The presence of a tomial notch rules out the Australian species in the genera *Trichoglossus* and *Glossopsitta*. The size of the rostrum precludes its placement in any genus except *Platycercus*, since *Apromiscus* and *Barnardius* are too large, and all others are too small. The local representatives of *Platycercus, P. elegans* and *P. eximius*, have similar-sized rostra, even though the postcranial elements of *P. eximius* are 10% smaller, on average, than those of *P. elegans*. The determination will, therefore, be made as *Platycercus* sp.

CUCULIFORMES

Cuculidae

Centropus colossus n. sp.

Materials. Slightly damaged left humerus (P.24240)

Diagnosis. The characters of the proximal end (e.g., small pneumatic foramina with little or no pneumatic fossa, and head tilted backwards and rotated clockwise)

Fig. 5. Stereoviews of the type specimen of *Centropus colossus* (P.24240): 1, anconal view; 2, palmar view.

and those of the distal end (e.g., the impression of the M. brachilis anticus being restricted to the extreme distal end, the ectepicondylar prominence located further proximally, and the distal end not flared laterally), distinguish this humerus from those of members of the Strigiformes and Caprimulgiformes and place it in the Cuculidae. It is here allocated to the Centropodinae, containing the type-genus *Centropus*, not for any single character but for its suite of characters (see Table 4). These characters include: shaft swollen where it contacts the humeral head ventrally; dorsal fossal arm broad and extending distally; scar for M. triceps humeralis (just below the pneumatic foramen) pronounced and rounded; humeral head swollen; pectoral crest with a continuous, even curve to the midline of the shaft's dorsal surface; muscle scars for M. pectoralis reduced; shaft expanded around a deep fossa M. brachialis; process flexorius narrow (medially) and twisted inwardly (medially), giving it an acute lateral point (see Fig. 5).

Holotype. Slightly damaged left humerus (P.24240). Collected under the supervision of Dr R. Wells in 1979. Measurements: total length, 73.0 mm; proximal width, 18.5 mm; distal width, 16.0 mm; width of shaft at midline, 7.0 mm; depth of shaft at midline, 6.0 mm.

Etymology. From Latin, *colossus*, of very great size. This fossil species is larger than any of the extant species in the genus *Centropus* and is one of the largest species of cuculid in the world.

Description. Humeral head swollen with small shelf overhanging capital insertion. Ventral tuberculum large; pneumatic foramen small with respect to the rest of the head. Shaft of humerus curved and stout. Dorsal supracondylar process low and rounded. Dorsal condyle proximodistal axis almost parallel with axis of shaft. Large process just medial to the sulcus of M. scapulotricipitalis (refer to diagnosis for all other characters).

Remarks. Many of the characters of the holotype of *Centropus colossus* are considered indicative of some degree of flightlessness (e.g., strongly twisted pectoral crest; reduced muscle scars; stout, curved shaft; etc.) as set out in Rich, McEvey & Baird (1985). Other characteristics of the specimen, such as the very deep M. brachialis fossa and the expanded distal end of the humerus, may be of some use in separating some groups within the Cuculidae. I have refrained from using any single character to determine the relationships of the element and, instead, have used a suite of characters.

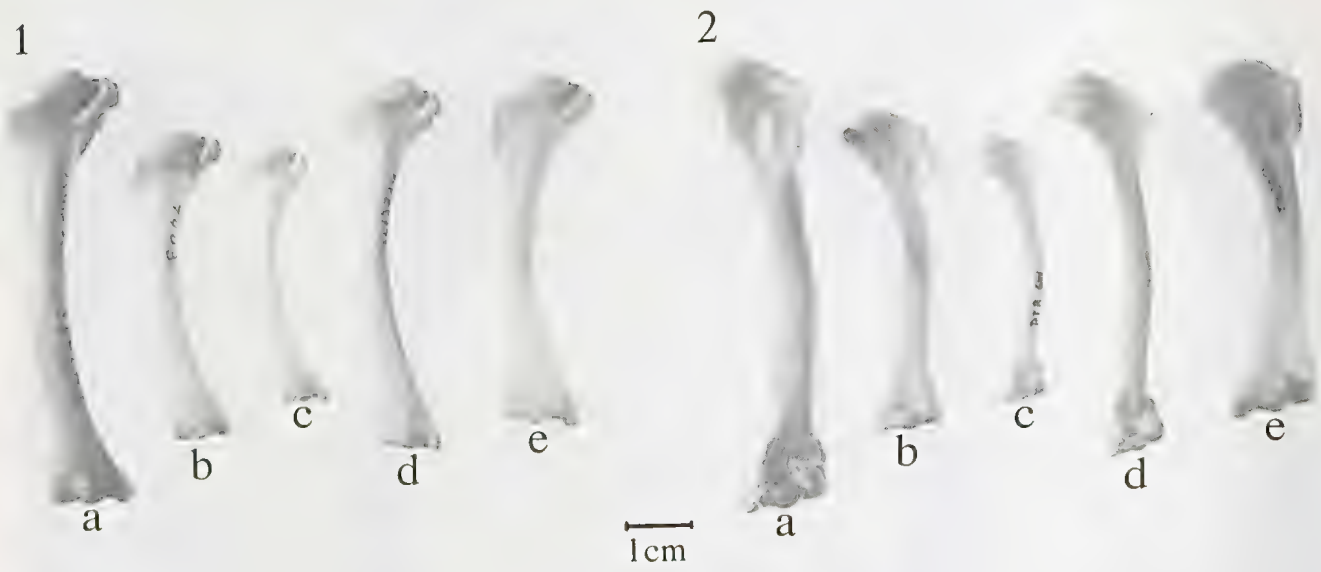

Fig. 6. Humeri of Cuculidae species illustrating differing manifestations of characters which are considered to be correlated with various levels of use of the wings for flight: 1, anconal view; 2, palmar view; a, *Centropus colossus* (P.24240); b, *C. menbeki* (AMNH 7403); c, *Geococcyx californianus* (PTR 574); d, *C. phasianinus* (QM 0.12726); e, *Carpococcyx renauldi* (UNMZ 223881).

Some of these characters are, in fact, common to other flightless species within the family, but in none do they manifest themselves in quite the same way (see Figs 5, 6 and Table 4).

The presence of the genus *Centropus* in this deposit extends its range much further south than is presently recorded. The only extant species of *Centropus* in Australia, *C. phasianinus*, is presently restricted to areas north of Sydney, New South Wales.

CORACIIFORMES

Alcedinidae

Dacelo novaeguineae

Material. Three complete right humeri (P.24437, 24438 & 24439), incomplete left ulna (P.24440), 2 incomplete right ulnae (P.24441 & 24442) and complete right radius (P.24443). The 8 specimens represent a minimum of 3 individuals. Subfamily previously unrecorded in the fossil record.

Remarks. The two Australian species within the genus *Dacelo* have humeri that are at least fifty percent longer than those of all other species in the family Alcedinidae occuring in south-eastern Australia. In the elements discussed, no diagnostic morphologic characters have been found to separate the two Australian species of *Dacelo*. However, the two species can be separated by comparison of the total lengths of these elements (see Table 5). The fossil material falls well within the size range for *D. novaeguineae* (see Table 5) and, therefore, has been assigned to that species. Currently, *D. novaeguineae* can be found along the whole of eastern Australia and the south-western tip of Western Australia, while *D. leachii* is restricted to the northern half of Australia.

PASSERIFORMES

Hirundinidae

Genus and species indeterminate

Material. Complete left humerus (P.24445)

Remarks. Of the four resident species of swallow in Australia (*Hirundo neoxena, Cecropis ariel, C. nigricans* and *Cheramoeca leucosternum*), three can be classed as speleophiles (*Hirundo neoxena, Cecropis ariel* and *C. nigricans*). All three of these cave-nesting species breed in the south-east of Australia, two frequently (*H. neoxena* and *Cecropis ariel*) and one infrequently (*C. nigricans*).

The Australian Hirundinidae, as a group, are osteologically diagnostic in their adaptions to life on the wing. Within the family, however, their uniformity poses many problems since they are so remarkably uniform, with regard to bone morphology and size, that species, and even genera, cannot be differentiated with confidence. Likewise, all three species occur within the south-east and, therefore, even biogeographical probability is ruled out as a method of identification, even though this is an unacceptable criterion. The material must, for the present, be assigned to

Table 4. Morphological character distribution of the humerus in the following specimens (– = character lacking; + = character present). **A**, Area of shaft ventral to the dorsal tubercle swollen as it meets the humeral head therefore not producing a shelf below the humeral head; **B1**, Pneumatic foramen small with the dorsal fossal arm broad and distally extending; **B2**, Muscle scar for M. triceps humeralis just below pneumatic foramina is pronounced (u) and rounded (v); **C**, Humeral head swollen; **D**, Pectoral crest with a smooth even curve to the midline of the shaft's dorsal surface (x), with deep furrow running ventral to the crest (y); **E**, Muscle scars for the attachment of the M. pectoralis are reduced; **F**, Shaft curved and stout; **G**, Fossa for M. brachialis deep and areas of shaft around fossa swollen; **H**, Process flexorious narrow (medially) and twisted inward (medially).

	A	B 1/2	C	D	E	F	G	H
Cuculiformes								
Musophagidae								
Musophaga violacea (MV B12565)	–	–/–	+	–	–	–	–	+
Cuculidae								
Cuculinae								
Clamator coromandus (USNM 343240)	–	+/+	–	–	–	–	–	–
Cuculus sparveroides (USNM 343990)	+	+/u	–	–	–	–	–	–
C. canorus (AMNH 5131)	–	+/+	–	–	–	–	–	–
C. variolosus (MV B77)	+	+/+	+	–	–	–	–	–
C. pyrrhophanus (MV B12657)	–	+/+	+	–	–	–	–	–
Chrysococcyx lucidus (MV B12697)	–	+/+	–	–	–	–	–	–
Scythrops novaehollandiae (CSIRO CUCS18)	+	–/u	–	–	–	–	–	–
Phaenicophaeninae								
Coccyzus erythropthalmus (PTR 454)	–	+/+	–	–	–	–	–	–
Piaya cayana (AMNH 4352)	–	+/+	–	–	–	–	–	–
Rhopodytes tristis (NMNH 344368)	–	+/+	–	–	–	–	–	–
Crotophaginae								
Crotophaga sulcirostris (PTR 675)	+	+/+	–	–	–	–	–	–
Neomorphinae								
Geococcyx californianus (PTR 574)	–	+/+	–	×	+	–	–	–
Carpococcyx renauldi (UMMZ 223881)	–	–/–	–	–	+	+	–	–
Couinae								
Coua caerulea (AMNH 10070)	+	–/–	+	–	+	+	–	–
Centropodinae								
Centropus goliath (USNM 557153)	+	+/+	+	+	+	+	+	+
C. menbeki (AMNH 7403)	+	+/+	+	+	+	+	+	+
C. phasianinus (QM 0.12726)	+	+/+	+	+	+	+	–	+
C. sinensis (USNM 344697)	+	+/+	+	y	+	+	+	+
C. monachus (USNM 322605)	+	+/+	+	y	+	+	+	+
C. colossus (P.24240)	+	+/+	+	+	+	+	+	+

Hirundinidae, indeterminate.

Orthonychidae

Orthonyx hypsilophus n. sp.

Material. Incomplete pelvis (P.24444).

Diagnosis. The fossil pelvis is similar to that of *Orthonyx* and differs from that of all other Australian passeriform genera in having the dorsal iliac crest divisible into two parts, anterior and posterior. The anterior part (median dorsal ridge) is a single crest composed of both the left and right ilia with no influence from the neural crests of the sacral vertebrae. The posterior parts (left and right) divide abruptly from the anterior part, each then running laterally, at right angles to the midline. The dorsolateral iliac crests are less than half as long as the anterior part of the dorsal iliac crest (see Fig. 7).

Compared with the pelvis of *O. temminckii* and *O. spaldingii*, that of the holotype is characterized by having the following: greater overall size (see Table 6); a dorsally more attenuate, deeper, anterior part of the dorsal iliac crest; very pronounced, fully enclosed pits, medial, and furrows, dorsal, to the acetabula; a concave iliac fossa; and a greater degree of sculpturing on the dorsal surface of the ilia (see Fig. 8)

Table 5. Humeri: total length measurements [GL] of several taxa of Alcedinidae whose present distributions (except *D. leachii*) encompass south-eastern Australia.

	mean	S.D.	min.	max.	N
Ceyx azureus	25.1	0.3	24.7	25.4	4
Dacelo novaeguineae	69.7	1.7	66.5	71.9	10
L-81	68.9	2.6	66.0	70.9	3
D. leachii	64.3	2.6	61.2	67.5	4
Halcyon pyrrhopygia	31.7	0.8	30.8	32.3	3
H. sancta	30.0	0.6	28.5	30.3	10

Holotype. Incomplete pelvis retaining all of the synsacrum, ilia and most of the acetabular portions of the os coxae (P.24444) (see Fig. 7). Collected under the supervision of Dr R. Wells in 1979. Measurements: total length of the synsacrum, 31.5 mm; width between the acetabula, 21.1 mm; depth from dorsalmost edge of the

Fig. 7. Stereoviews of the type specimen of *Orthonyx hypsilophus* (P.24444): 1, ventral view; 2, dorsal view; 3, lateral view.

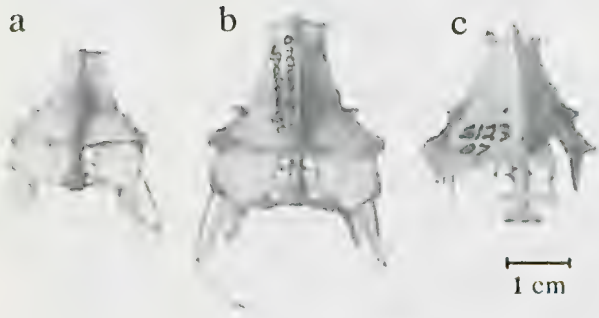

Fig. 8. Dorsal views of *Orthonyx* spp. pelves demonstrating the construction of the dorsal iliac crests and the structural differences amongst the three species: a, *O. temminckii* (AM 0.57019); b, *O. spaldingii* (QM 0.21124); c, *O. hypsilophus* (P.24444).

Table 6. Lengths of synsacra [LV] from *Orthonyx* spp.

	mean	S.D.	min.	max.	N
O. temminckii	20.3	0.8	19.3	21.2	4
O. spaldingii	27.5	0.6	27.1	27.9	2
O. hypsilophus	31.5	–	–	–	1

anterior part of the dorsal iliac crest to ventral synsacrum, 11.8 mm.

Etymology. The specific name *hypsilophus* is derived from the Greek *υψι*, high, and λοφος, crest or ridge, the combination to be regarded as adjectival in form and declined to agree with the masculine gender of *Orthonyx*. The new species has a comparatively high median dorsal ridge as measured against those in the two extant species of *Orthonyx*.

Description. Both antitrochanters and posterior parts of the dorsal iliac crest maintain strong anteriolaterally projecting shelves. First, fourth, fifth and thirteenth parapophyses enlarged, with the fourth and fifth very swollen. All other parapophyses lamellate but still very much evident. In lateral view, the acetabula lie ventral to the synsacrum and slightly anterior to its median point. Thirteen parapophyses in the synsacrum.

Remarks. The morphological variation that occurs within the genus is probably the result of structural changes associated with increased overall size. Characters that might have otherwise proven useful in determining the phylogeny of *O. hypsilophus* can be demonstrated as being variable within each species, and grading from one species to another. These characters include; the pits and furrows medial to the acetabulae; the concave iliac fossa; the presence of thirteen, instead of twelve, vertebrae in the synsacrum (as determined by counting the numbers of parapophyses); and the first,

fourth, fifth and thirteenth parapophyses enlarged. In the smallest species, *O. temminckii*,the pits exist as very shallow, open-ended indentations with the furrows lacking; the iliac fossa are convex; the synsacrum is made up of either twelve or thirteen fused vertebrae, with additional vertebrae fused to either the anterior or posterior margins; and only the first, fourth and twelfth parapophysed are enlarged. In the medium-sized *O. spaldingii*, the pits are relatively deeper, but still remain open-ended; the iliac fossa are flat; the synsacrum is made up of either twelve or thirteen vertebrae and, depending upon the number of vertebrae, enlarged parapophyses include the first, fourth and twelfth, or first, fourth, fifth and thirteenth (respectively). The additional vertebra is added to the front of the synsacrum and is associated with a swollen fourth parapophysis. *Orthonyx hypsilophus*, the largest of the three species, demonstrated a greater development in all four characters.

Within the genus, the os coxae demonstrates a greatly expanded surface area in the iliac fossa and foreshortened ischia. The development of this unusually shaped pelvis is associated with an equally unusual method of foraging. Zusi (1978), in describing the feeding behaviour of *O. spaldingii*, states that, "when clearing litter the birds pushed leaves to the side with one foot and then the other, each time shifting the weight of their bodies over the supporting foot." This is unusual for, as Zusi mentions, "a single sideways sweep began with the foot forward beneath the bird's throat and extended to the side in an arc of ninety degrees or more". A similar feeding behaviour has been described for *O. temminckii* (Boles & Shields, 1980). The expanded surface area of the iliac fossa accomodates a greatly expanded M. iliotrochantericus caudalis, which originates over the whole of the cranial surface of the iliac fossa. The pits medial to the acetabulae in *O. hypsilophus* are formed by the increased structural support of the origin of M. iliotrochantericus medius. The area of origin of this muscle is barely raised above the dorsal surface of the ilia in *O. temminckii* but is very pronounced, forming a pedestal, in *O. hypsilophus*. Increased surface area of the origins of M. iliotrochantericus cranialis and M. iliotrochantericus caudalis are interpreted from the enlarged muscle scars, for the first, and increased depth of the iliac crest, for the second, in the specimen of *O. hypsilophus*. Differences in the pelvis of *Orthonyx* from that of all other passeriforms are assumed to be adaptions to this unusual method of foraging. Within the genus, the pelvis of *O. hypsilophus* is adapted to greater strength in the clearing of debris during foraging.

The presence of this genus in South Australia during the late Quaternary has interesting biogeographical implications. The two extant species of *Orthonyx* live chiefly in rainforest along the north-eastern seaboard (Blakers *et al.*, 1984), particularly those forests with a deep humus layer (Hindwood, 1934) allowing for adequate forage. *Orthonyx temminckii* does venture out into thickets of *Lantana* and *Rubus* (Lantana and Blackberry) along roadsides bordering rainforest (Keast, 1944; pers. obs.). What seems to be important is the low intensity of light necessary to cover the birds' movements. Both species seem to survive only in those areas which provide a sufficiently dense canopy, as well as adequate accumulation of litter on the forest floor.

In south-eastern Australia, particularly western Victoria and south-eastern South Australia, mammalian faunas indicating wet forests were last recorded in the Early Pliocene (Turnbull & Lundelius, 1970). By the Late Pliocene the rainforests of much of Australia had been replaced by vegetation dominated by xerophytic genera (e.g., *Eucalyptus* and *Casuarina*) (Galloway & Kemp, 1984). The vegetation of south-eastern Australia, since then, has been mainly a mosaic of wet sclerophyl, dry sclerophyl and savanna woodland. In the 'Green Waterhole Cave' area, as mentioned in the introduction, eucalypt woodland was dominant from beyond radiocarbon dating to 35,000 y.B.P. From 35,000 until 6,000 y.B.P., the more xeric-adapted *Casuarina* dominated woodlands (Dodson, 1975). It is here suggested that *O. hypsilophus* lived in *Melaleuca* thickets that border wet areas, such as lakes, ponds and streams. Throughout southern Victoria and south-eastern South Australia, *Melaleuca ericifolia, M. squarrosa* and *Leptospermum lanigerum* form a very dense, closed scrub, with canopy cover of 70 to 100 percent (Specht *et al.*, 1974). Therefore this habitat would have provided both sufficent canopy and litter. *Melaleuca* is recorded from the area of south-east South Australia throughout the last 50,000 y.B.P. (Dodson, 1975). If this is true, then the genus *Orthonyx* can no longer be considered strictly adapted to rainforest. It is now apparent that the radiation within this genus was ecologically greater than is currently demonstrated. The extinct species was probably adapted to drier habitats, evolving from a rainforest inhabiting ancestor sometime during the Pliocene desiccation.

Acanthizidae

Dasyornis broadbenti

Material. Complete right humerus (P.24446), complete right tibiotarsus (P.24447). The 2 specimens represent a minimum of 1 individual. Family previously unrecorded in the fossil records.

Remarks. Most of the terrestrially adapted birds in Australia have similarly shaped humeri, and this particular shape, presumably, is an adaptation to this mode of life (Rich, McEvey & Baird, 1985). The humeri of *Dasyornis* can be separated from the other similarly adapted birds by possessing a scar for the insertion of the M. scapulohumeralis anterior that is distally extending and acute at its distal end; a flattened humeral head at an angle greater than ninety degrees from the shaft, measured distally; a bulbous internal tuberosity; and a strongly curved pectoral crest. The tibiotarsus of *Dasyornis* differs from that of other similarly adapted birds by its less pronounced tubercle for the attachment

Table 7. Humeri (H) [GL] and tibiotarsi (T) [La]: length measurements of the three species of *Dasyornis* (* = complete skeletal specimens are lacking for both *D. longirostris* and *D. brachypteris*, therefore measurements for these two species were taken from X-rays of skins. These measurements can only be used as rough comparisons as the exact orientation of the element relative to the camera is unknown.)

		mean	S.D.	min.	max.	N
D. longirostris	(H)	19.3	–	–	–	1
	(T)	*33.9	1.3	33.0	34.8	2
D. brachypterus	(H)	*19.5	–	–	–	1
	(T)	*38.3	0.4	38.0	38.5	2
D. broadbenti	(H)	24.5	0.5	24.1	25.0	6
	(T)	46.7	1.8	44.4	48.1	5
L-81	(H)	23.4	–	–	–	1
	(T)	50.1	–	–	–	1

of M. femorotibialis interior, a laterally flattened medial condyle, a swollen lateral condyle, and a high cnemial crest.

Of the three recognised species of *Dasyornis, D. broadbenti* is by far the largest (see Table 7) and the fossil elements are, therefore, attributed to that species. *Dasyornis broadbenti* is the only one of the three species now occuring in the south-east of South Australia, although prehistorically at least two species occurred in that region.

Meliphagidae

Manorina melanocephala

Material. Complete cranium (P.24448). Genus previously unrecorded in the fossil record.

Remarks. This specimen was found on the water surface and, though no fleshy tissue remained, it may be of more recent origin than the rest of the deposit. The skull can be identified as *Manorina* by its short, broad cranium (length, 27.0 mm; width, 20.8 mm) as well as the presence of: a single bar acting as the interorbital partition; a robust process dorsal to the temporal fossa; and a sculptured bone surface, reaching from the temporal fossa to the cerebral prominence. *Manorina melanocephala* may be separated from *M. flavigula* by its larger size and its geographical distribution.

Corvidae

Corvus sp.

Material. Left mandibular ramus (P.24449), anterior sternal fragment (P.24450), complete left ulna (P.24451), complete right radius (P.24381), incomplete left femur (P.24452), and complete right and 2 incomplete left tibiotarsi (P.24453–24455). The 7 specimens represent a minimum of 2 individuals.

Remarks. The Australian representatives of the family Corvidae can be separated allometrically from the Cracticidae by their larger ulnae, sterna and femora. The tibiotarsi have rounded distal trochleae (viewed laterally), as opposed to the semi-circular shape in cracticids. Because of the round trochleae, the intercondylar fossae of corvids are more proximodistally expanded. Mandibles are identified by their more elongate (not squared) internal articular processes.

If present day distributions are taken into account, then three corvids are possible for the locality, *C. coronoides, C. mellori* and *C. tasmanicus*. With the small number of skeletal specimens available and the dubious identity of many of these (see Rowley, 1970) it is not possible to identify the fossil material to species level. Therefore, the determination will be left at *Corvus* sp.

DISCUSSION

The 'Green Waterhole Cave' deposit is taphonomically unique among cave sites recorded in Australia. Of those fifteen cave deposits whose taphonomic influences are determinable, 73% were carnivore accumulated or show evidence of some form of carnivore activity, 20% are subaerial pitfalls/death traps and 7% were fluvially accumulated (Baird, in press). Each of the above taphonomic groups states the main accumulating force, although the deposits may have been under the influence of several accumulating forces. The L-81 material is, at present, covered by water which was possibly the accumulating force behind the deposit. Although drowned caves are relatively common, water is rarely proposed as an accumulating force.

Cave formation in limestone is often dependent upon the flow of water through the rock. The different water flow types, therefore, present the most satisfactory way of classifying these caves (Sweeting, 1973: 158). The two most common forms of caves are phreatic and vadose. As defined by Sweeting (1973), phreatic caves are those caves formed within the zone of limestone which lies at or just beneath the level of permanently saturated rock, and vadose caves are those caves formed by water circulating under gravity above the level of permanently saturated rock. The bulk of cave genesis typically occurs at or above the saturation level in the karst limestone. During marine transgressions, caves would be formed at greater heights within the carbonate strata than those formed during the previous regressions, assuming equivalent rises in the ground water levels. Those caves topographically lower in the stratigraphy would be drowned by the rising water level. During eustatic lows, the same caves would be left high and dry. A similar effect can occur through minor tectonic uplift. As can be surmised from this sequence of events, at various times any one level of caves may be submerged or exposed depending on fluctuating saturation levels.

Given this brief history of cave formation, it can be seen that, although a cave is drowned, it does not necessarily mean that water was the accumulating force for its deposits. For example, on Oahu in the Hawaiian Island chain, there is a drowned cave (50-0a-B6-139) whose contents include beautifully preserved specimens of a *Corvus* sp. and a *Chaetoptila* sp.. Because of their

high degree of association it was suggested that the animals entered the cave during a dry phase, died and were subsequently covered by water (Olson & James, 1982). The end result is the same as in L-81, except that the degree of association is greater in the Hawaiian cave. The lack of fully articulated skeletons in L-81 suggests that either there has been postdepositional movement in L-81, or a different taphonomic history has been involved. Even though postdepositional movement has occurred, there are other reasons for thinking that the taphonomic processes behind the deposit are unusual. This can be clarified by comparing the L-81 faunal material to other cave faunas from south-eastern Australia

Because carnivores show bias in the types of prey they accumulate, and since 73% of all cave deposits in south-eastern Australia are attributed to carnivores, there tends to be great similarity in faunal lists from one deposit to another (Baird, in press). Large psittaciforms, however, have only been recorded from a few caves and have never formed a large part of any cave fauna. Of the thirty-seven cave deposits mentioned for the south-east of Australia (including N.S.W., Vic. and S.A.; Rich & van Tets, 1982) only two, outside of L-81, contained large psittaciforms. An additional specimen of *Cacatua tenuirostris* (AM # F53469) has recently been recorded from another drowned cave in the south-east of South Australia, The Pines, L-61. I propose that the reasons for the differences in the faunal lists between the 'norm' and L-81 lie in the taphonomy of the deposit. If the faunal list (see Table 8) is divided into five parts (i.e., flocking species, terrestrial species, carrion eaters, speleophiles and indeterminate) it can be seen that at least two groups, the flocking species and the terrestrial species, dominate (83% of all individuals), lending support to the hypothesis that water is the accumulating agent behind this deposit.

Of the sixteen species of birds in the deposit, six species commonly flock (37%) (*Calyptorhynchus magnificus, C. lathami, Callocephalon fimbriatum, Cacatua tenuirostris, Platycercus* sp., *Corvus* sp.. [Cacatuidae undetermined not included]), four species are terrestrial (25%) (*Gallinula mortierii, Centropus colossus, Orthonyx hypsilophus, Dasyornis broadbenti*), three species are possible carrion eaters (19%) (undescribed accipitrid, *Falco* cf. *berigora, Dacelo novaeguineae*), one species is a speleophile (6%) (Hirundinidae indet.), which leaves *Phaps chalcoptera* and the *Manorina melanocephala* undetermined (13%). If we use the same groups but, instead of determining percentage from the total number of species, we use the total number of identifiable individuals (53), the picture becomes clearer. The flocking species now make up (70%) of the total, the terrestrial species (13%), the carrion eaters (9%), the speleophiles (2%), and the undetermined (6%). Given that the flocking species make up such a large part of the total, and that the individual elements lack any diagnostic damage indicative of the action of carnivores, it seems likely that there was some other process at work in the accumulation of the deposit.

Table 8. List of the avian specimens known from Green Waterhole Cave, with the scientific and common names, number of specimens (N) and minimum number of individuals (MNI).

	N	MNI
Accipitridae		
n. sp.	7	1
Falconidae		
Falco cf. *berigora* (Brown Falcon)	1	1
Rallidae		
Gallinula mortierii (Tasmanian Native-Hen)	10	4
Columbidae		
Phaps chalcoptera (Common Bronzewing Pigeon)	1	1
Phaps sp.	1	1
Cacatuidae		
Calyptorhynchus magnificus (Red-tailed Black Cockatoo)	4	1
C. lathami (Glossy Black Cockatoo)	1	1
Callocephalon fimbriatum (Gang-gang Cockatoo)	1	1
Cacatua tenuirostris (Long-billed Corella)	127	31
indeterminate	18	5
Platycercidae		
Platycercus sp. (Rosella sp.)	1	1
Cuculidae		
Centropus colossus n. sp. (Giant Coucal)	1	1
Alcedinidae		
Dacelo novaeguineae (Kookaburra)	7	3
Hirundinidae		
indeterminate	1	1
Orthonychidae		
Orthonyx hypsilophus n. sp. (Extinct Logrunner)	1	1
Acanthizidae		
Dasyornis broadbenti (Rufous Bristlebird)	2	1
Meliphagidae		
Manorina melanocephala (Noisy Miner)	1	1
Corvidae		
Corvus sp. (Raven sp.)	7	2

For water to have been the accumulating force, the animals must first have been attracted to the cave, restricted to the area of water and then forced to enter the water. Pledge's (1980) explanation has the animals entering the cave in search of water and, because of a two metre drop, being trapped in the lower reaches of the cave and drowning while attempting to escape. How would this be relevant to the avian content of the deposit?

Attraction to bodies of water similar to the drowned cave is quite frequent in birds. As noted by several authors (Craig & Powers, 1976; Chilgren, 1979), birds in search of water in the western U.S. will arrive at watering tanks and in the frenzy of landing will try to perch on floating debris and each other. A small number

of birds would subsequently be soaked. If there were no access to dry ground, then the birds could eventually drown. There is evidence in the U.S. of Western Meadowlarks (*Sturnella neglecta*), Common Crows (*Corvus brachyrhynchos*) and American Kestrels (*Falco sparverius*) lining the bottoms of stocktanks. Similarly, stock tanks in northern South Australia have been seen, by the author, to be carpeted with the bodies of a *Corvus* sp. and the occasional Little Corella (*Cacatua sanguinea*). Budgerigars (*Melopsittacus undulatus*) have been recorded as drowning when large flocks come down to drink (Forshaw, 1969: 282). Although *Phaps chalcoptera* is a flocking species, its method of approaching a drinking spot is different from most in that it usually lands some distance away and walks to the water (Frith, 1982: 224). The proposed explanation for the accumulation of the avian parts of the L-81 material is similar to that mentioned above. The birds would enter the cave during drought periods, try to land on floating debris not capable of keeping them afloat, wet their feathers, and eventually drown. As compared with Pledge's explanation, the only difference would be the final reason for drowning. The animals collected by this means of accumulating force would, therefore, reflect local population size and flocking habits, and not the bias of predators.

As was found with the mammalian fauna, the avian fauna seems to be made up of both extant and extinct species, which for a 'Late' Pleistocene/Holocene deposit is unusual. Geographical range extensions were recorded for two species, *Gallinula mortierii* and *Calyptorhynchus lathami*, and two genera, *Centropus* and *Orthonyx*. Three species new to science were found: one accipitrid, one cuculid and one passeriform. The accipitrid has yet to be diagnosed, but from all accounts is larger than any extant Australian member of the family (Rich, pers. comm.). The coucal, *Centropus colossus*, is unusual both for its enormous size, being one third larger than its closest Australian relative, and its advanced stage of flightlessness. The passerine, *Orthonyx hypsilophus*, is also unique for its adaptions to terrestriality and its large size. The three new species and the *Cacatua tenuirostris* material seem to be remnants of Pleistocene gigantism, so well known from the other continents (Marshall & Corruccini, 1978). The extinction of large mammals in Australia has been generally thought to have been confined to the period between 26,000 and 15,000 y.B.P. (Horton, 1984) and it is suggested that the large extinct avian species are possibly of similar age.

Relative dating of the site is difficult, for the deposit itself provides no tangible measures of time. Data on sea level transgressions provide a maximum age of opening of 125,000 y.B.P. Dating by faunistic analysis is difficult. The animals are either peculiar to the deposit, which suggests a date greater than 15,000 y.B.P., or ubiquitous to the whole south-eastern corridor, and therefore not suggestive of any date. In any case, because the deposit is slumped and, therefore, of mixed ages, the best one can do using the fauna is try to put a maximum age on the deposit, which at this stage is probably greater than 15,000 y.B.P..

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APPENDIX

Measurements of all the species in the Cacatuidae whose present distribution includes south-eastern Australia (within 137°–152°S and 33°–39°E). Specimens used were from localities within this defined zone and therefore assumed to belong to the local subspecies of each species. Measurements are arranged according to taxonomic order following Condon (1975).

Additional material of *Cacatua sanguinea* were added at the last moment. These data increased the sample population but did not change the statistics for the species appreciably. The corresponding sections in Figure 4 were, therefore, left unchanged.

	mean	S.D.	min	max	N
CRANIUM					
Length [LP]					
Calyptorhynchus magnificus	52.0	4.1	48.5	56.5	3
C. lathami	46.2	1.1	45.0	47.3	4
C. funereus	50.1	1.5	47.8	52.2	7
Callocephalon fimbriatum	39.2	1.1	36.7	39.6	8
Cacatua roseicapilla	37.3	2.0	34.1	40.5	9
C. tenuirostris	43.6	1.6	41.5	44.6	9
C. sanguinea	40.7	1.1	39.0	42.6	11
C. leadbeateri	44.5	1.2	42.4	45.0	4
C. galerita	51.2	3.6	48.0	56.5	10
Width [SBO]					
Calyptorhynchus magnificus	35.8	2.0	33.5	37.0	2
C. lathami	36.9	0.7	36.4	37.9	4
C. funereus	30.6	1.4	29.0	32.5	7
Callocephalon fimbriatum	27.3	1.4	24.9	28.5	8
Cacatua roseicapilla	23.2	1.6	20.4	24.6	10
C. tenuirostris	27.9	1.2	26.5	29.1	9
C. sanguinea	26.5	1.0	25.0	27.8	11
C. leadbeateri	29.5	0.6	29.0	30.0	4
C. galerita	35.2	2.6	31.4	40.3	10
HUMERUS					
Length [GL]					
Calyptorhynchus magnificus	84.3	5.9	75.4	88.5	4
C. lathami	68.5	2.7	66.4	72.2	4
C. funereus	76.2	3.8	67.3	80.2	8
Callocephalon fimbriatum	55.7	1.9	53.5	58.4	8
Cacatua roseicapilla	58.4	2.1	55.5	62.0	11
C. tenuirostris	71.3	1.1	70.0	72.5	7
C. sanguinea	67.4	2.4	63.0	70.5	12
C. leadbeateri	69.5	1.7	68.7	71.5	3
C. galerita	88.0	2.8	85.0	92.0	6
Proximal width [Bp]					
Calyptorhynchus magnificus	21.8	1.1	20.0	23.0	3
C. lathami	17.0	0.7	16.3	17.8	4
C. funereus	19.7	0.8	18.5	20.3	7
Callocephalon fimbriatum	13.3	0.6	12.4	14.2	8
Cacatua roseicapilla	15.0	0.7	14.4	16.0	11
C. tenuirostris	18.2	1.6	17.2	18.5	7
C. sanguinea	16.5	0.7	15.0	17.4	12
C. leadbeateri	15.8	0.8	15.7	17.2	3
C. galerita	21.4	0.4	21.0	22.3	6
ULNA					
Length [GL]					
Calyptorhynchus magnificus	99.5	5.0	91.5	102.5	4
C. lathami	82.1	3.8	79.0	87.2	4
C. funereus	89.9	4.9	79.4	95.3	8
Callocephalon fimbriatum	66.8	2.2	63.9	70.5	8
Cacatua roseicapilla	69.0	2.5	65.3	73.0	11
C. tenuirostris	85.5	1.6	82.9	86.9	7
C. sanguinea	82.2	3.0	76.0	86.0	12
C. leadbeateri	83.0	2.5	80.5	85.7	3
C. galerita	106.7	3.5	102.1	111.5	7
CARPOMETACARPUS					
Length [GL]					
Calyptorhynchus magnificus	61.1	3.3	56.6	64.0	4
C. lathami	49.6	2.9	47.0	52.9	4
C. funereus	56.8	2.7	50.7	59.2	7
Callocephalon fimbriatum	39.6	2.0	36.7	42.3	7
Cacatua roseicapilla	43.5	1.8	41.8	46.9	11
C. tenuirostris	50.1	1.0	49.0	51.6	7
C. sanguinea	46.2	1.8	43.0	48.2	12
C. leadbeateri	47.3	1.2	46.0	47.8	3
C. galerita	56.4	1.3	55.0	58.5	7
FEMUR					
Length [GL]					
Calyptorhynchus magnificus	55.3	2.7	51.4	58.0	4
C. lathami	44.4	1.8	42.8	46.8	4
C. funereus	54.2	2.3	50.6	57.8	8
Callocephalon fimbriatum	38.3	1.2	36.5	39.9	8
Cacatua roseicapilla	40.9	1.7	38.1	45.0	11
C. tenuirostris	51.9	1.2	50.5	53.5	8
C. sanguinea	47.5	1.2	45.5	49.5	12
C. leadbeateri	45.2	3.3	42.2	48.5	3
C. galerita	59.6	1.7	57.0	61.2	6
TIBIOTARSUS					
Length [La]					
Calyptorhynchus magnificus	77.3	5.0	69.7	81.5	4
C. lathami	61.2	2.2	59.1	64.2	4
C. funereus	76.3	4.2	67.8	81.2	8
Callocephalon fimbriatum	56.1	2.5	52.9	58.8	7
Cacatua roseicapilla	59.5	2.4	54.9	63.3	10
C. tenuirostris	73.6	1.9	71.2	76.0	7
C. sanguinea	67.8	1.9	64.5	71.0	12
C. leadbeateri	64.2	2.9	62.0	67.3	3
C. galerita	84.3	2.9	80.5	87.3	6
TARSOMETATARSUS					
Length [GL]					
Calyptorhynchus magnificus	26.6	2.1	24.2	28.5	4
C. lathami	18.4	0.8	17.5	19.4	4
C. funereus	27.3	1.2	25.1	28.9	7
Callocephalon fimbriatum	17.4	0.8	16.8	18.3	7
Cacatua roseicapilla	21.5	1.1	19.2	23.0	10
C. tenuirostris	24.9	0.6	24.0	25.5	7
C. sanguinea	23.7	0.7	22.6	24.4	11
C. leadbeateri	23.0	0.9	21.9	23.7	3
C. galerita	27.3	0.8	26.5	28.7	6
Distal width [Bd]					
Calyptorhynchus magnificus	14.3	0.9	13.4	15.0	4
C. lathami	11.3	0.5	10.8	11.7	4
C. funereus	12.9	0.3	12.4	13.6	7
Callocephalon fimbriatum	10.3	0.6	9.5	11.3	7
Cacatua roseicapilla	9.7	0.5	9.2	10.0	10
C. tenuirostris	12.1	0.2	12.0	12.2	7
C. sanguinea	11.6	0.6	10.7	12.5	11
C. leadbeateri	12.8	0.8	12.0	13.4	3
C. galerita	16.1	0.8	15.5	16.8	6
CORACOID					
Length [LM]					
Calyptorhynchus magnificus	42.8	2.2	39.8	44.5	4
C. lathami	36.2	1.7	34.2	38.3	4
C. funereus	41.4	2.4	37.6	44.5	8
Callocephalon fimbriatum	30.4	0.9	29.5	31.2	8
Cacatua roseicapilla	35.9	1.5	34.4	39.0	11
C. tenuirostris	42.3	0.9	40.6	43.0	8
C. sanguinea	39.9	1.5	38.0	42.0	12
C. leadbeateri	37.8	0.4	37.5	37.9	2
C. galerita	46.6	1.9	43.5	48.5	6

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